NUTRIENT UPTAKE AND INTERNAL CYCLING IN A MATURE PINE STAND

LIM MENG TSAI

Ph.D.

UNIVERSITY OF EDINBURGH

1979

I hereby declare that this thesis has been composed by myself from results of my own work.

October 1979.

CONTENTS

ABSTRACT

Nutrient uptake and the degree of internal cycling in a mature Scots pine stand were investigated and the changes in the intensity of internal cycling with nutrient availability were determined. This involves the estimation of biomass, nutrient content and transfers from older tissues to new growth as well as transfers between the plant and the soil.

The biomass of the above-ground parts of trees estimated from regressions was 120.8 tonnes/ha. This consisted of 11.2 t needles, 20.7 t branches and 87.3 t bole. Total annual production of biomass obtained by summing all current year tissues was 17.0 t/ha. This was made up of 5.6 t needles,3.2 t branch, 6.7 t bole wood, 0.6 t bole bark and 0.8 t cones. Concentrations of N, P, K, Ca and Mg in the various plant tissues are low. Above-ground parts of trees contain 331.7 kg N, 34.5 kg P, 211.5 kg K, 139.1 kg Ca and 46.4 kg Mg per hectare. The nutrient requirement, estimated as contents of nutrients in the annual production of biomass, was 115.2 kg N, 12.8 kg P 62.1 kg K, 20.8 kg Ca and 9.9 kg Mg per hectare.

Annual input of nutrients in rain water amounts to 1.6 kg N, 0.4 kg P, 4.6 kg K, 8.2 kg Ca and 1.6 kg Mg per hectare. Leaching from the foliage, estimated by relating contents in the rainfall to amounts in throughfall, was found to contribute 0.4 kg N, 0.3 kg P, 8.6 kg K, 6.5 kg Ca and 3.1 kg Mg per hectare per year.

4.5 t fine litter produced annually, of which 3.5 t consisted of needle litter, returned a total of 36.6 kg N, 2.2 kg P, 7.6 kg K, 12.1 kg Ca and 2.0 kg Mg per hectare.

After accounting for all possible transfers from the tissues, the amounts retranslocated annually were estimated at 61.1 kg N, 8.6 kg P, 46.5 kg K and 1.4 kg Mg per ha. Ca was not retranslocated, but accumulated at a rate of 8.8 kg/ha/year.

Annual uptake, estimated as the difference between requirement (amount in current year tissues) and retranslocation, amounts to 48.2 kg N, 4.6 kg P, 28.4 kg K, 29.0 kg Ca and 6.5 kg Mg per hectare per year. These values correspond to 44% of the requirement for N, 35% of the requirement for P, 38% of the requirement for K, 83% of the requirement for Mg and over 1.4 times the requirement for Ca because of accumulation of Ca in the older tissues.

An experiment was also conducted to determine the changes in the pattern of internal cycling of N with its availability in the soil. With increased supply of N, uptake increases and retranslocation decreases, and when the soil supply of N decreases, retranslocation increases as a result of decreased uptake. These changes are reflected in changes in litter production - litter production in fertilised plots decreased in the first year after treatment, but increased in the second year while in N depleted plots, litter production increased in the first year.

CHAPTER 1.

INTRODUCTION

1.1. Introduction

The increase in demand for wood and other forest resources has resulted in more intensive management of forests which includes better utilisation and even complete-tree harvesting (Young, 1964, 1967, 1975; Hakkila, 1971, 1973; Keays, 1971; Alestalo, 1973), planting with faster growing species, planting on poor sites (Ovington, 1960; Rennie, 1966) and the use of fertilisers (Leaf and Leonard, 1976; Mayhead, 1976). The proper application of such management techniques, however, requires an understanding of the productivity of the forest and the nutrient cycles that operate within it, as well as the factors which affect them (Ovington, 1960; Curlin, 1970; Malkonen, 1973, 1976; Kimmins and Krumlik, 1976; Ulrich, 1976).

1.2. Statement of Problem

Various aspects of the productivity, mineral nutrition and nutrient cycle in Scots pine have been studied in Britain (Ovington, 1957a, 1957b, 1959a, 1959b, 1959c; Wright and Will, 1958) and elsewhere (Malkonen, 1974; Lehtonen, 1977, 1978; Olszowski, 1976a, 1976b). The earlier studies were prompted by concern that tree crops might deplete the soil resources (Rennie, 1956). They therefore concentrated on estimating the quantities of organic matter and nutrients and made comparisons of the total

amounts in the trees and of the trunks which were harvested, with the total amounts in the soil. Later studies have included estimates of various transfers operating within the forest ecosystem and, in particular, have concentrated on the nutrient budget for the whole system.

While some recent studies on Loblolly pine and Douglas fir have shown that nutrient cycling internal to the trees does occur (Switzer and Nelson, 1972; Turner, 1975), and is important in mature trees and in areas of low fertility, very little work has been conducted on other conifers to investigate internal cycling and to determine whether retranslocation is a general phenomenon among conifers. While some evidence on retranslocation from Scots pine needles exists (Malkonen, 1974; Ericsson, 1978) there is no evidence in the literature of retranslocation in the branches and the bole wood nor is there any estimate of the amounts which are retranslocated from the needles.

1.3. Aims of Study

This study aims to determine

a) the degree and pattern of internal cycling in a mature Scots pine stand, and
b) the relationship of the internal cycling pattern to the availability of nutrients.

Five major nutrients were selected for study. N and P were selected as they are commonly limiting to such an extent that the ability to retranslocate these elements would be of great

ecological advantage. K, Ca and Mg were also selected as they are important in metabolism; K and Ca in particular, for their contrasting mobility to retranslocation and pattern of accumulation (Epstein,1971).

The investigation of internal cycling requires the assembly of nutrient budgets and this in turn requires detailed analyses of biomass, growth, turnover and throughfall.

The second objective has been met by creating conditions of enhanced supply of nitrogen (by fertiliser application) and depleted supply (by adding sawdust and sugar which should reduce available nutrients as they become locked up in the decomposer biomass).

1.4. Literature Review

1.4.1. Nutrient Cycles

The cycle of nutrients in a plant ecosystem refers to the circulation of nutrient elements between the various parts of the system - the plants and the soil - and the environment. It is a complex process consisting of a variety of subcycles or polycycles (Ovington, 1968) operating between the different parts of the system. Broadly, these subcycles may be classified into three types - the geological, biogeochemical and biochemical cycles (Switzer and Nelson, 1972).

1.4.1.1. Geological Cycle

The geological cycle involves the ecosystem and its

surroundings - the atmosphere and the underlying rocks and soil. Nutrients are added into the system by chemical weathering of the underlying rocks as well as by rain, which sometimes does contain significant amounts of certain nutrients (Henderson and Harris, 1973; Madgwick and Ovington, 1959; Carlisle, Brown and White, 1967). Nutrients may also be lost from the system through underground leaching and drainage (Feller, 1977) as well as by the harvesting of the crop (Ovington, 1962; Kimmins and Krumlik, 1976).

1.4.1.2. Biogeochemical Cycle

The biogeochemical cycle refers to the cycle operating between plants and other living organisms and the soil-humus complex. Nutrients are actively and often selectively absorbed by plants for growth. Some of these nutrients are retained in various plant structures while others are returned to the soil through the death of plants or parts of plants and leaching by rain, as well as waste products from herbivores.

1.4.1.3. Biochemical Cycle

The biochemical cycle operates within the plants and involves transfers and redistribution of nutrients between the different parts of the plants. Nutrients like carbon, nitrogen and phosphorus are withdrawn from older tissues and retranslocated to the shoots or cambium for new growth, so that older tissues generally have lower concentrations of such nutrients than the newly formed

tissues. Other nutrients like calcium, on the other hand, are continuously accumulated, so that older tissues have higher concentrations of them than younger ones (Epstein, 1971).

1.4.2. Transfer Processes

In order to assess the role and importance of the biogeochemical and biochemical cycles in the growth of plants, it is necessary to estimate the amounts required for growth, the amounts taken up by the plants from the soil and the amounts returned to the soil by the plants.

1.4.2.1. Requirement

Requirement is defined as the total amount of a nutrient that is required annually for the production of new growth (Turner, 1975; Switzer and Nelson, 1972). In conifers it is estimated as the sum of the contents of the nutrient in all the current or first year growth of foliage, branch and wood as well as of cones. This method, however, tends to underestimate the total requirement since current bark growth on the main stem and branches as well as male cone production are not considered. Using this method, Malkonen (1974) estimated that 45 and 47-year old Scots pine in Finland required 22.5 - 27.8kg N, 2.7 - 3.2kg P, 10.3 - 15.4kg K and 7.3 - 11.6kg Ca per ha for annual production.

1.4.2.2. Retranslocation

Retranslocation or redistribution refers to the total amount

of the nutrients that are redistributed in a year within the plants. Ideally, the amounts involved should be estimated by analysing the tissues annually from the time they are formed to the time they die. Turner (1975) however, assumed that older tissues had concentrations of nutrients of current tissues when they were current. Retranslocation is estimated as equal to the total amount of a nutrient present in all the living tissues in a year minus the total amount of that nutrient present in the second and older living tissues in the following year, plus the amounts that are lost through death or leaching in the intervening year (Switzer and Nelson, 1972).

1.4.2.3. Uptake

Uptake is the total amount taken up by the plant through its roots annually. The origin of the nutrients may be the soil, the humus or even the litter layer. Uptake may be estimated indirectly in a number of ways. Ovington (1959a) working on a series of stands of increasing age, determined uptake as the difference in content of two stands of consecutive age classes divided by the difference in age of the two stands. Heilman and Gessel (1963b) and Malkonen (1974) however, estimated uptake as the sum of the current annual requirement and the annual litter production. Miller, Miller and Pauline (1976) improved their estimates of uptake by including losses through leaching. These methods however, do not take into account the retranslocation which may alter the estimates considerably. To overcome this, Turner (1975)

estimated uptake as the difference between requirement and retranslocation plus the amount lost through leaching.

Uptake of nutrients by trees increases with age until the canopy begins to close, which may take between 20 and 30 years (Ovington, 1959a; Turner, 1975). Thereafter, uptake declines. Ovington (1959a) estimated the mean annual uptake of Scots pine as 78 kg N, 7 kg P, 33 kg K, 41 kg Ca and 7 kg Mg per hectare. The maximum current uptake of 180 kg N, 13 kg P, 65 kg K, 83 kg Ca and 18 kg Mg per hectare occurred in 20 to 23-year old stands.

1.4.2.4. Return

Return refers to the total amount returned annually by the trees to the soil and forest floor through litterfall and death of various parts of plants such as roots, and/or leaching. The return of organic matter and nutrients through litterfall is very well documented (Bray and Gorham, 1964). Such measurements of litter production are however, restricted to fine litter components such as foliage, twigs, bark and fruits and flowers. Estimates of return of larger items such as dead branches and even of trees are however, more difficult to obtain as their pattern of fall is uneven and patchy and also, a large fraction of dead branches are retained on both living and standing dead trees. While fine litter production may range from 0.6 to 6.9 t/ha/an (Bray and Gorham, 1964), Ovington (1959b) found that stands between 35 and 55 years produce approximately 5.3 t/ha annually.

The return of nutrients by leaching is somewhat more difficult to assess, for although input of nutrients by rainfall and throughfall are well documented (Madgwick and Ovington, 1959; Will, 1959; Swank and Henderson, 1976; Carlisle, Brown and White, 1967), there are few studies which attempt to separate the effects of leaching from the canopy from the contribution by aerosols (White and Turner, 1970; Miller, Cooper and Miller, 1976). When rainwater passes through the canopy the concentration of nutrients such as N and P may decrease due to absorption by the leaf or leaf-surface organisms, while concentrations of other nutrients such as K may increase as a result of leaching from the leaves. Miller, Cooper and Miller (1976) plotted the content of nutrients in throughfall against the content in the incoming rainfall and proposed that the intercept on the y-axis represented the amount leached while White and Turner (1970) used particle traps to estimate the input of aerosols during dry weather and subtracted this input from the total amount in throughfall to obtain the amounts leached.

1.4.2.5. Ratios

By relating estimates of the various parameters of the nutrient cycle, such as uptake and retranslocation to the requirement of the plants, measures of dependence of the trees on these different parameters may be obtained. A high uptake to requirement ratio indicates that the soil and forest floor are the major sources of the nutrients required for growth whereas a high retranslocation

to requirement ratio suggests that a high proportion of the requirement is met by sources from within the trees (Turner, 1975). Relating the input from rain to requirement provides a measure of the importance of rain to the nutrient budget of the ecosystem (Norton and Young, 1976).

Internal cycling has been estimated to contribute up to 47%, 60% and 22% of the total annual requirement of N, P and K respectively in Loblolly pine and Douglas fir (Switzer and Nelson, 1972; Turner, 1975).

1.4.3. Biomass of Stands

1.4.3.1. Estimation

In order to estimate the magnitudes of the various transfers in the nutrient cycle and since nutrients are incorporated in organic matter, it is necessary to determine the distribution of organic matter and the nutrient contents of the components. Several methods have been used to estimate the biomass of a stand of trees, the most commonly used being the harvesting of a sample of trees according to one of the procedures described below:-

a) Selection of a representative area, followed by a complete harvest of all the trees in the plot: the biomass per hectare may then be obtained by multiplying the total weight of trees in the sample plot by either the appropriate area factor or tree number factor. This method assumes that the area as well as the trees selected are representative of the whole stand.

b) Selection of trees with mean chosen dimensions such as

diameter at breast height (d.b.h.), girth at breast height (g.b.h) or basal area: the average weight of such trees is assumed to be the mean weight of the trees in the stand. Multiplying this value by the density of the stand gives the biomass per unit area. This method, however, underestimates the biomass of the stand (Attiwill and Ovington, 1968; Baskerville 1965 ; Crow , 1971) since the weight of the tree based on the mean girth or diameter at breast height is less than the weight of the tree based on the mean basal area, which in turn is less than the weight of the tree which is based on the mean weight or volume of the stand.

c) Selection of trees of varying sizes from different size classes: data from such samples may be treated in two ways. In the first, as in b) above, trees of each size class are assumed to weigh the same as a sample tree from that size class and the total weight of all the trees in that size class is the product of the number of trees in that class in the stand and the weight of the sample tree of that class. The biomass of the stand is then obtained by summing the total weight of all the size classes. The second method of treating the data is to establish regression equations relating the weights of the trees or their components to their corresponding girths, diameters or basal area (Madgwick, 1976). Such equations may then be used to predict the weight of any tree in the stand from their girths or diameters and by summing up these individual weights, the biomass of all the trees in the stand may be obtained.

This last method, known as allometry (Ogawa, Yoda and Kira,

1961) or dimensional analysis (Whittaker and Woodwell, 1968) is currently the most widely used. In order to achieve linearity and better fit and to facilitate statistical analysis, the regression equations are based on the log-transformed data instead of the original data (Mountford and Bunce, 1973; Krumlik and Kimmins, 1973; Rochow, 1974; Beauchamp and Olson, 1973). The dimensions most commonly used as the independent variable are diameter at breast height (Baskerville, 1966 ; Dice, 1970; Maclean and Wein, 1977), girth at breast height (Ovington and Madgwick, 1959; Attiwill and Ovington, 1968) and the product of the square of the diameter and height ($D^2.H$) (Ogawa, Yoda and Kira, 1961; Madgwick and Satoo, 1975).

Based on theoretical considerations of log-transformation and re-transformation, Baskerville (1972), Beauchamp and Olson (1973) and Mountford and Bunce (1973) suggest that the values obtained by re-transformation of the log values to arithmetic values tend to be underestimates. To correct for this bias, they recommend the use of a correction factor based on the variance about the regression line. Madgwick (1971) and Madgwick and Satoo (1975), however, found from intensive simulated sampling of actual weights, that with this correction, values tend to be overestimated, and they suggest that as the bias from re-transformation is small compared to the overall variation in the estimate of biomass, the correction factor may be ignored.

Estimates of individual weights of trees obtained from regressions may differ quite considerably from their actual

weights but the predicted weight of a stand obtained by summing individual estimates may not differ too widely from the actual biomass since some of the predicted values are underestimates while others are overestimates, and with a sufficiently large number of trees in a stand, the total sampling error is reduced (Dice, 1970). Studies comparing the accuracy of the various methods show that the regression technique coupled with individual tree summation consistently gives the highest and also the most accurate estimate of stand biomass (Ovington and Madgwick, 1959; Baskerville, 1965; Ovington, Forrest and Armstrong, 1968; Attiwill and Ovington, 1968; Crow , 1971). Further, destructive sampling is minimal so that for a large number of stands, the regression method is the least time consuming (Ribe, 1973).

1.4.3.2. Distribution of Biomass

As a plant grows, the biomass of its various components increases. This increase is however, not similar in all the components. The relative proportions of the various components vary with age. This variation has been studied by determining the distribution of biomass in trees of different ages (Ovington, 1957b; Switzer, Nelson and Smith, 1966; Forrest and Ovington, 1970) In young trees, the leaves make up a large proportion of the total biomass but in older trees, they account for less than 10% of the total biomass (Ovington, 1957b; Forrest and Ovington, 1970). This decrease in the proportion of leaves is due to the closing of the canopy with age, as well as the steady increase in biomass of the main stem, which may account

for over 60% of the total biomass in mature stands (Ovington, 1957b).

Scots pine plantations over 35 years old in Britain contain in each hectare, 7.2 - 9.8 t needles, 9.6 - 12.25 t branches and 96.7 - 129.2 t main stems (Ovington, 1957b) while in Finland, plantations between 45 and 47 years old contain 3.5 - 4.4 t needles, 6.8 - 7.4 t branches and 30.4 - 60.9 t of boles in each hectare (Malkonen, 1974).

1.4.4. Nutrient Content of Stands

1.4.4.1. Method

The amounts and distribution of nutrients are obtained by multiplying the biomass of the different components with the concentrations of the various nutrients in that component. Studies have shown that nutrient levels may be influenced by a number of factors such as the age of the tree and the tissue, the position in the tree from which the samples were taken, the time of sampling and the soils on which the trees are growing (White, 1954; Wells and Metz, 1963; Miller, 1966)

In spite of this variation in nutrient levels, Young and Carpenter (1976) in an intensive comparison of nutrient concentrations in different parts of seven species of trees found that there were few significant differences between samples taken from different parts of the same tree. They suggested that as few as four samples, representing the four major components - leaves, branch, bole and root - from three trees would be sufficient to provide reliable estimates of the nutrient

concentrations in trees.

1.4.4.2. Content in Needles

For nutrient analyses needle samples are usually taken from the top, middle and base of the living crown. Needles may be further subdivided into samples of different ages. Generally, first or current year needles have higher concentrations of N, P and K but lower concentrations of Ca, than older needles (Ovington, 1959a; Malkonen, 1974; Webber, 1977). The concentrations of N and P may increase slightly in the second year but thereafter decrease slowly with age, and prior to leaf abscission, decrease rapidly because of retranslocation. The level of K decreases rapidly with age because of leaching by rain-water, while the concentration of Ca increases due to continuous accumulation. Scots pine needles contain 0.7 - 3.0% N, 0.06 - 0.40% P, 0.30 - 1.60% K, 0.05 - 0.58% Ca and 0.06 - 0.18% Mg (Ovington, 1959a; Carlisle and Brown, 1968; Malkonen, 1974).

1.4.4.3. Content in Branches

Branches, like needles, are also sampled from the top, middle and base of the crown, often together with the needles. They may be further divided into different diameter classes. Concentrations of N, P and K tend to increase with the height up the tree (Malkonen, 1974) as well as with decreasing age of the branches (Ovington, 1959a), while the concentrations of Ca and Mg do not show any such trends. Scots pine branches contain 0.20 - 1.20% N, 0.05 - 0.18% P, 0.10 - 0.90% K, 0.12 - 0.35%

Ca and 0.03 - 0.20% Mg (Ovington, 1959a; Malkonen, 1974).

1.4.4.4. Content in Wood

Stem wood and stem bark are often analysed separately and samples consisting of complete discs or segments of them are usually taken at regular heights up the bole. As in the branches, the concentrations of N, P and K tend to increase with height up the tree. The concentrations of these nutrients have also been shown to increase with distance from the centre of each disc (Barker, 1966) with the outermost ring of wood having the highest concentration, suggesting that retranslocation also takes place in the stem wood. Based on complete discs, Scots pine stem wood contain 0.06 - 0.4% N, 0.004 - 0.05% P, 0.035 - 0.30% K, 0.06 - 0.20% Ca and 0.01 - 0.04% Mg (Ovington, 1959a; Malkonen, 1974) and the bark contains 0.3 - 0.4% N, 0.05 - 0.06% P, 0.19 - 0.23% K and 0.32 - 0.55% Ca (Malkonen, 1974).

1.4.4.5. Total

By summing up the nutrient content in all the different components of the trees in the stand, the total weight of nutrients bound in the crop may be obtained. In British Scots pine plantations between 35 and 55 years old, the following ranges have been reported : 453 - 471 kg N, 41 - 51 kg P, 150 - 241 kg K, 272 - 355 kg Ca and 64 - 70 kg Mg per hectare (Ovington, 1959a) while in 45 and 47 year old stands in Finland, there are 109 - 150 kg N, 11.5 - 15.0 kg P, 45 - 73 kg K and 51 - 100 kg Ca (Malkonen, 1974).

1.4.5. Effects of Nutrient Availability on Nutrient Cycling

With increasing demand for wood and other forest resources, the use of fertilisers to enhance growth as well as to improve areas of low fertility is increasing. While the growth and production response to fertiliser treatment is well known (Heilman and Gessel, 1963a; Olszowski, 1976a; Olszowski and Warteriesiewicz, 1976; Safford, Young and Knight, 1977), less is known of the fate of the nutrients applied and their effects on the nutrient cycles (Turner, 1975; Wells, Nicholas and Buol, 1975; Ulrich, 1976). With the application of nitrogen fertilisers, needle retention is increased and a higher fall of needle litter results after two or more years (Wells, Nicholas and Buol, 1975; Miller, Cooper and Miller, 1976). Requirement and uptake also increase with fertiliser application (Heilman and Gessel, 1963; Turner, 1975).

In contrast, very few studies on the effects of a deficiency on the nutrient cycle have been conducted (Turner, 1975), although the effects of deficiency of various nutrients on growth are well known (Epstein, 1971). Decreased amounts of nitrogen in the soil resulted in lower uptake and higher retranslocation (Turner, 1975).

CHAPTER 2.

MATERIALS AND METHODS

2.1. Introduction

Information on the distribution of organic matter and nutrients as well as production and losses are essential for the study of nutrient cycling. In order to demonstrate that retranslocation (or redistribution) occurs and to estimate the amounts involved as well as the amounts taken up from the soil, the various components of the tree have to be subdivided into classes of different age. The needles and branches are each subdivided into three age classes, namely, one-year old, two-year old and three-year old and over tissues. The bole is separated into the bark and five wood fractions which correspond to ring numbers 1, 2, 3, 4 to 10 and 11 and over, counting inwards from the cambium.

Regressions relating the biomass of the component to girth size are first established by careful dismantling and weighing of a sample of trees. The biomass of the different components are then estimated using these regressions and their nutrient contents determined by analysing samples of these various components for the different nutrients. Annual production and nutrient requirements are also estimated from the distribution of current year tissues, while losses of organic matter and nutrients are determined from litter production and leaching from the canopy.

From the various estimates of production and losses, the amounts cycled internally and the amounts taken up from the soil are obtained.

2.2. Site

Devilla Forest is located approximately on latitude 56° 7'N and longitude 3° 40'W. The area has an undulating topography and lies between 15 and 100m above sea level. The soil varies from a podsol with a distinct iron pan near the tops of ridges to a gley-podsol at the lower levels, with glacial till above the underlying sandstone. The study area (National Grid Reference NS982908) is near the top of one of the lower ridges and slopes very gently in a north-south direction.

The Meteorological Office rainfall map of Britain shows that the area is bounded by the 850 and 900mm isohyets and this coincides with the rainfall measured during part of the study period. The mean temperature is about 8.6°C while the average minimum is 5°C and the average maximum is 12°C (Anderson and Fairbairn, 1955).

The area was established around 1931 with (2+1) Scots pine nursery stock. The history of management and development of the area prior to 1965 is not clear as the Forestry Commission records have been lost. However, by studying the height increments between whorls on the trees, it was found that growth prior to approximately 1943 was very poor (Plate 1). Conditions in an open scrubland adjacent to the study area suggest that the

Plate 1. Tree with unbrashed lower whorls showing poor growth prior to 1943 . BH - Breast-Height; W43 - 1943 whorl.

Plate 2. View in Plot T3 showing a litter-trap and a drain (to the left of the litter-trap).

Plate 3. View in Plot T4 showing an uprooted tree and ferns growing in the gap.

poor growth might be due to the water-logged gley soils. The improved growth since then suggests that the drains present in the area (Plate 2) could have been dug around 1943. From the evidence of stumps in the area in 1965, when the area was first used by the University, it seemed that the first thinning might have taken place in 1958 or 1963 (Cousens, pers. comm.). The trees were marked for another thinning in 1968 but this was delayed after extensive wind damage (Plate 3), until 1971 when the trees were re-marked for thinning. Extraction racks were also opened up in 1971 in areas adjacent to the study plots.

The forest floor consists of large areas of only litter. In more open areas, bracken (Pteridium aquilinum (L.) Kuhn), Broad Buckler-fern (Dryopteris dilitata (Hoffm.) A. Gray), wavy hairgrass (Deschampsia flexuosa (L.) Trin.) and mosses (Plagiothecium, Leucobryum and Sphagnum spp.) are found, while isolated bushes of Rhododendron sp., Vaccinium sp. and Calluna sp. are also present occasionally. Three birch saplings (Betula sp.) found within the sample plots are above breast height and have been included in the enumeration with the pines.

2.3. Methods

2.3.1. Plot Enumeration

Five rectangular plots measuring 20m by 25m and one 20m square plot were established in the forest area in November 1976 and all live trees within the plots were marked at breast height (1.3m)

with red paint and numbered with a plastic label. In January and February 1977 the girths of all the trees were measured with a metal tape to the nearest mm. The heights of all the trees were also measured with a Blume-Leiss altimeter, using a horizontal distance of 15m since the trees were mostly between 10 and 15m in height.

In November and December 1977, the girths and heights of the trees in the six plots were remeasured. Although this second enumeration was done in November and December instead of January and February 1978, the results are unlikely to be different as there is practically no girth or height increment between November and May.

2.3.2. Sampling of Trees

In March and April 1977, a sample of 10 trees with girths ranging from 20cm to 80cm from outside the experimental plots was felled, weighed and sampled for dry weights as well as nutrient content determinations. The crown whorls and the bole were treated separately. The boles were cut into 10 logs of equal lengths, each of 0.1 height of the tree. The logs were weighed using Salter balances of 10, 30 and 50kg capacity, and from the base of each log a 2cm thick disc was cut for dry weight and nutrient analysis. Each live crown whorl was weighed separately and whorl numbers 1, 2, 3, 4, and every fourth living whorl, from the top, were collected and taken back to the laboratory where the needles, twigs and branches were each separated into the three age classes.

Branches without needles were considered as dead and all such branches from one tree were amalgamated and one sample taken for dry weight determination as recommended by Rennie (1966). All samples were dried at 80°C in force draught ovens for at least four days since constant weight was only attained after a minimum of three days. From the percentage dry weight of the disc samples, the dry weights of the log sections were obtained assuming that the mean percentage dry weight of a log is intermediate between those of the two consecutive sample discs. From the percentage dry weight of the sample whorls based on the total whorl the percentage dry weight of the intermediate whorls was estimated assuming a linear change in the percentage dry weights between successive sample whorls. From the relative percentage of needles and twigs, the amounts of needles and twigs were also calculated. The amounts of first, second and third year needles and twigs and branches were also calculated from the proportions in the sample whorls and interpolated for intermediate whorls.

Alternate sample discs were polished and the widths of the bark, first, second and third rings from the outside, as well as the widths of the 4 - 10th ring band and the radii of the remaining core were measured under a low powered binocular microscope. Measurements were made in two directions at right angles to each other, using a steel rule with 0.01 inch markings. The measurements were converted to mm and the areas of the rings calculated assuming a perfectly circular cross-section. As the bark has a density different from that of the wood, it is

not possible to convert the ring areas directly into biomass. To overcome this, the densities of the bark and the wood were determined using the method of displacement of water, and the area of the bark modified by the appropriate ratio of the densities. The areas of the different rings were then expressed as percentages of the total cross-sectional area. The weights of the rings in each log section were then obtained as the product of the weight of the log and the corresponding percentages of the cross-sectional areas of the appropriate rings. The weights of the rings in the shoot section were obtained assuming that the rings form the bases of a series of cones inside one another.

Results of a preliminary study on the concentrations of nutrients showed that for needles and branches, there was no significant difference between samples from different whorls, but there were differences between samples of different ages. Therefore,different aged needles and branches were sampled from the third, fourth, eighth and sixteenth whorls. Samples were ground in a hammer mill and stored in plastic tubes. The preliminary study also showed that there were significant differences in the concentrations of most nutrients inwards from the bark as well as up the tree. Since the change up the tree was less significant than the radial change, and in view of the objectives of the study, disc samples from the base, 0.2 and 0.6 of the height of the trees were analysed. The discs were cut into wedges and the bark and wood rings separated using a scalpel. Each ring sample was sliced radially into thin flakes

which were used directly for analyses.

2.3.3. Rainfall and Throughfall

In order to estimate the rainfall and throughfall and the input of nutrients into the plots, three rain-collecting funnels were set out approximately 3m apart in a straight line along the long axis of each plot, in each of the six plots as well as in a clearing within the forest. Although variations in throughfall measurements are generally high (Kimmins, 1973), only three collectors were used as this was considered the maximum number which could be handled satisfactorily. Each of the collectors consists of a glass funnel (10cm diameter) leading into a 1-litre reagent bottle which was one-third buried to prevent it from toppling over.

The rainfall and throughfall samples were collected every four weeks. The volume of water was measured with a measuring cylinder and a sample of at least 150ml was collected into plastic bottles for nutrient analyses. The solutions were then filtered under pressure and 25ml concentrated and digested in the presence of sulphuric acid and then cleared with hydrogen peroxide. The residue was then made up to 5ml and the solution used directly for the determination of nitrogen and phosphorus. The concentrations of the other nutrients were determined using the filtered solutions.

2.3.4. Litter Production

To estimate the transfer of organic matter and nutrients from the trees to the soil, five litter traps were set out in each of the six plots, with four at the corners of a square approximately 10m by 10m such that the traps were at least 5m from the edge of the plots, and the fifth trap in the middle of the square. Each litter trap consists of a funnel constructed of a plastic bag suspended over a thick wire ring (of internal area $0.05m^2$) at a height of 0.5m from the ground. Holes were made at the base of the bag to allow the drainage of rainwater. Collection involves the removal of the whole bag and its replacement by another. Litter samples were dried in the bags at $80^{\circ}C$ in the oven and then sorted into needles, cones, twigs and a miscellaneous fraction. These fractions were weighed before they were ground up for analyses.

2.3.5. Treatment to alter Nitrogen supply

In order to assess the changes in the nutrient cycle in response to the supply and availability of soil nitrogen, two of the plots were treated with nitrogen, two with saw-dust and the remaining two left as controls. Ammonium nitrate (34%N) was added at the rate of 150kg N per hectare as recommended by the Forestry Commission (Mayhead, 1976). Super phosphate (20%P) was also added at the rate of 20kg per hectare to maintain the N:P ratio of the soil nutrient supply. Sawdust and sugar were added at the rate of 900kg sawdust and 30 kg

sugar per hectare respectively to encourage the development of soil microorganisms. Since these soil microorganisms compete with the trees for the nutrients in the soil, it was hoped that their enhanced development would reduce the supply of nutrients, especially of N, available to the trees.

In March and April 1978, two trees from each of the six plots were harvested in a similar way to the first ten trees (Section 2.3.2.). One tree of girth about 35cm and another with girth of about 65cm were chosen such that they were at least 5m from the edge of the plot to reduce the edge effect, especially in the fertilised and sawdust treated plots.

2.3.6. Chemical Analyses

All samples were oven dried at 70°C for at least 24 hours prior to being weighed for analyses. 0.1 - 0.2g of samples were digested with 2ml concentrated sulphuric acid with 0.5 - 1.0ml hydrogen peroxide at 350°C. Cleared digests were made up to 50 ml with distilled water and the solutions used directly for all determinations. Nitrogen was determined by the ammonium dichloro-isocyanurate colour reaction (Crooke and Simpson, 1971) and phosphorus by the reduced phosphomolybdate colour reaction using an autoanalyser. Potassium was determined by emission spectrophotometry and calcium and magnesium by absorption spectrophotometry (Allen,Grimshaw,Parkinson and Quarmby, 1974).

2.3.7. Calculations

Regressions based on the log transformed values for girths and weights were calculated with log(girth) as the independent variable. The equation has the form,

$$\log(\text{weight}) = b \times \log(\text{girth}) + c.$$

Weights of individual trees and their components were estimated by substituting their respective girths into the equations and then taking the antilogs of the estimated 'log(weight)' values (Beauchamp and Olson, 1973). The total weight of trees/components in the plot was obtained by summing all the individual weights predicted by the equations from the individual girths. The results are presented on a per hectare basis.

The variance sometimes used in the factor to correct for bias is the variance of the transformed data of the biomass (Mountford and Bunce, 1973; Satchell, Lindley and Hibberd, 1971), but the correct variance is the mean square of deviations from the regression (Snedecor, 1956), which is obtained as follows,

$$s^2_{Y.X} = \Sigma (Y - \hat{Y})^2 / (n - 2)$$

where Y and $\hat{Y}$ are the actual and predicted log values of the weights. The correction factor is calculated as follows,

$$c = \text{exponential} (s^2_{Y.X} / 2)$$

and is estimated for the major components obtained in 1977.

This variance cannot, however, be converted to an arithmetic equivalent by taking its antilog as it is based on a different distribution (ie. arithmetic vs. logarithmic).

An estimated variance in arithmetic value is, however, obtained by using the arithmetic values of the actual and predicted weights instead of their log equivalents (Malkonen, 1974). The standard error of the sampled mean (Sokal and Rohlf, 1971) in arithmetic scale is then calculated as follows:

$$SE\ \hat{Y} = \sqrt{(s^2_{Y.X} / n)}$$

CHAPTER 3.

RESULTS AND DISCUSSION I. DISTRIBUTION OF DRY MATTER IN THE STAND

3.1. Introduction

As nutrients are bound to organic matter, the determination of the distribution of organic matter is a prerequisite for investigations on nutrient distribution as well as the study of nutrient cycling. In this chapter, the results of field enumeration will be presented first, followed by the results obtained from the destructive sampling of trees. The next section deals with biomass estimated from girth data obtained during field enumeration using the regressions obtained in the previous section, while the final section deals with annual production and accumulation of dry matter. The girth data of all the trees in the six plots is listed in the Appendix (Table I).

3.2. Stand Characteristics

3.2.1. Yield Class

The mean top height of the trees shows that the stand is intermediate between General Yield Classes 6 and 8, as defined by the Forestry Commission (Hamilton and Christie, 1971) (Table 1). If, however, the height increment during the period of restricted growth and the number of years involved (approximately 1.2m and 12 years, respectively), are subtracted from the measured top height and the actual age in the assessment, as recommended by Hamilton and Christie (1971), the stand would fall into General Yield Class 10. This is probably a more appropriate classification of the stand as the current height increments and basal area are

Table 1. Characteristics of sample plots in 1977 and 1978.

Year	Plots	Density (No./ha)	GBH(cm) Mean	GBH(cm) Max	GBH(cm) Min	Basal Area (m^2/ha)	BA Increment (m^2/ha)	Top Height (m)
1977	C1	1820	44.47	75.60	19.40	31.72		12.92
	C2	1560	51.84	87.10	19.20	37.03		13.74
	T1	1660	47.92	94.00	21.20	34.15		14.32
	T2	1440	50.82	85.10	17.00	33.16		14.08
	T3	1280	53.86	87.80	15.50	32.33		13.90
	T4	1740	43.47	82.70	17.10	30.04		13.98
	Mean	1583	48.32	94.00	15.50	33.00		13.82
1978	C1	1760	46.10	77.50	19.40	32.43	0.71	
	C2	1500	53.73	88.80	21.40	37.94	0.91	
	T1	1640	48.89	96.10	21.40	35.54	1.39	
	T2	1420	52.02	86.30	17.10	34.60	1.44	
	T3	1220	56.05	88.60	15.50	33.54	0.81	
	T4	1640	45.48	85.00	17.10	30.90	0.86	

more similar to those in a younger General Yield Class 10 stand than a stand of similar age belonging to General Yield Class 6 or 8.

3.2.2. Stocking

The mean density of the stand is 1583 trees/ha (Table 1). This is slightly higher than the average density of a Yield Class 10 Scots pine stand at 35 years, prior to thinning (1455 trees/ha). The densities in the individual plots are very variable, and range from 1280 to 1825 trees/ha. This high variation has resulted because the irregularly spaced gaps left by trees which died as a result of waterlogged conditions during the first decade or so, were not restocked.

3.2.3. Mortality

During the period between the first and second enumeration, between 1 and 5 trees died in each of the six plots. (This is equivalent to between 20 and 100 trees/ha.) (Table 1). While most of these trees belong to the supressed category and have girths at breast height of less than 30 cm, two had girths over 30 cm but below 45 cm. Some of the dead trees had been slash-marked for thinning in 1968 but were not re-marked and felled in 1971.

3.2.4. Tree Sizes

While the mean girths from each of the six plots do not vary much, the girths of individual trees are very variable, with the

maximum girth being more than 6 times that of the minimum (Table 1). This high variation in girth sizes is probably greater than would normally be found in a well managed even-aged stand, and is related to the development of the stand at Devilla. The gaps that resulted from the mortality of trees in the waterlogged conditions and which were not re-stocked, enabled adjacent trees to grow vigorously and develop into large dominants. The last thinning in 1971 also contributed to this high variation in girth size in that many of the smaller trees were not removed, probably because they were not yet of commercial size.

3.2.5. Growth Increment

The girths of some of the larger trees increased by as much as 2.1 cm in a year, while some of the smaller trees did not show any girth increment (Table 1). This zero increment could have resulted from the flaking of the bark, no measurable increase in girth, or errors in the initial measurement. The increase in the mean girth, which varied between 0.92 and 2.19 cm, was lowest in the fertilised plots and highest in the saw-dust treated plots. This increase in the mean girth is however not a good indicator of growth or response to treatment since deaths of the smaller trees would automatically increase the value of the mean. The change in basal area, on the other hand, is a better indicator as it integrates density and tree size. The increase in basal area varied between 0.71 and 1.44 m^2/ha and was markedly greater in the fertilised plots than in the other plots. Negative height increments resulting from differences in instruments and sighting direction however,precludes the consideration of increments in heights.

3.3. Sample Trees

3.3.1. Selection

The sample trees were selected in such a way that there were trees in nearly every 10 cm girth size class above 20.0 cm, and such that the overall mean girth of all the samples approximated to the mean girth of all the trees in the six plots. This was to ensure that the errors in the regressions arising out of the displacement of the sample mean from the population mean would be minimised. The resultant mean girth of the sample trees was 0.02 cm above the mean girth of all the trees in the plots (Table 2).

3.3.2. Size Range

The smallest tree sampled had a girth of 20.0 cm and weighed 8.15 kg, while the largest sample tree had a girth of 80.7 cm and weighed 210.75 kg. As the girth size of individual trees in all the plots range from 15.5 cm to 94.0 cm, the variation in the biomass of individual trees in the study area would be over 25-fold. The smallest tree was supressed whereas the two largest trees sampled, with girths of 80.7 cm and 69.0 cm, were dominant and codominant respectively.

3.3.3. Proportions of Component Parts

3.3.3.1. Major Components

The proportion of live needles in the trees does not vary

Table 2. Dimensions and weights of the major components of the smallest and largest sample trees **and the mean for the 10 sample trees. Percentage contribution of each component to the total live weights are in brackets.**

Characteristics	smallest	largest	mean	$SE_{(Y.X)}$	CV (%)
Girth (cm)	20.00	80.70	48.34		
Height (m)	8.07	14.10	11.82		
Weights (kg)					
Needle	0.66 (8.10)	17.46 (8.29)	7.07 (8.90)	0.57	1.8
Branch	1.12 (13.79)	54.79 (26.00)	14.33 (15.74)	1.22	8.5
Total Crown	1.78 (21.90)	76.76 (36.42)	21.88 (24.88)	1.48	6.8
Bole	6.37 (78.10)	133.99 (63.58)	54.58 (75.12)	2.46	4.5
Total Live (above ground)	8.15 (100.00)	210.75 (100.00)	76.45 (100.00)	1.38	1.8
Dead Branch	0.81	9.33	6.90		

$SE_{(Y.X)}$: Standard Error of the sampled means (Rohlf and Sokal, 1971)

CV : Coefficient of Variation based on $SE_{(Y.X)}$.

much with tree size and averages 8.9% of the total above ground biomass (Figure 1). Although cones were not found on a number of the sample trees, they averaged slightly less than 1% because the largest tree had a very large crop which constituted over 2% of the total dry weight of the tree. The proportion of bole decreases from about 80% of the total biomass in trees with girths below 40 cm to between 65 and 70% in the larger trees, while the proportion of live branches increases from 10 - 14% in the smaller trees to over 20% in the larger ones. This enhanced development of the crown of the larger trees reflects the exploitation of these trees of the gaps in the canopy left by the trees which died during the period of unfavourable growth.

3.3.3.2. Crown Components

First year needles make up an average of 53% of all the needles while second and third year needles average 35 and 12% respectively (Figure 2). Of the total branch weight, the first and second year twigs account for 7.1% and 6.8% respectively, and the older branches make up the remaining 86.1% (Figure 3). Although these proportions do not show any marked trend with increasing size of the tree, a slightly above average proportion of third year needles is found in the bigger trees. The higher retention of third year needles seems to be related to the favourable light conditions at the top of the crown of dominant trees. Although Scots pine needles may persist up to four years (Carlisle and Brown,1968), very few 4-year old needles were found in the Devilla samples and so were amalgamated with the 3-year old needles. The retention

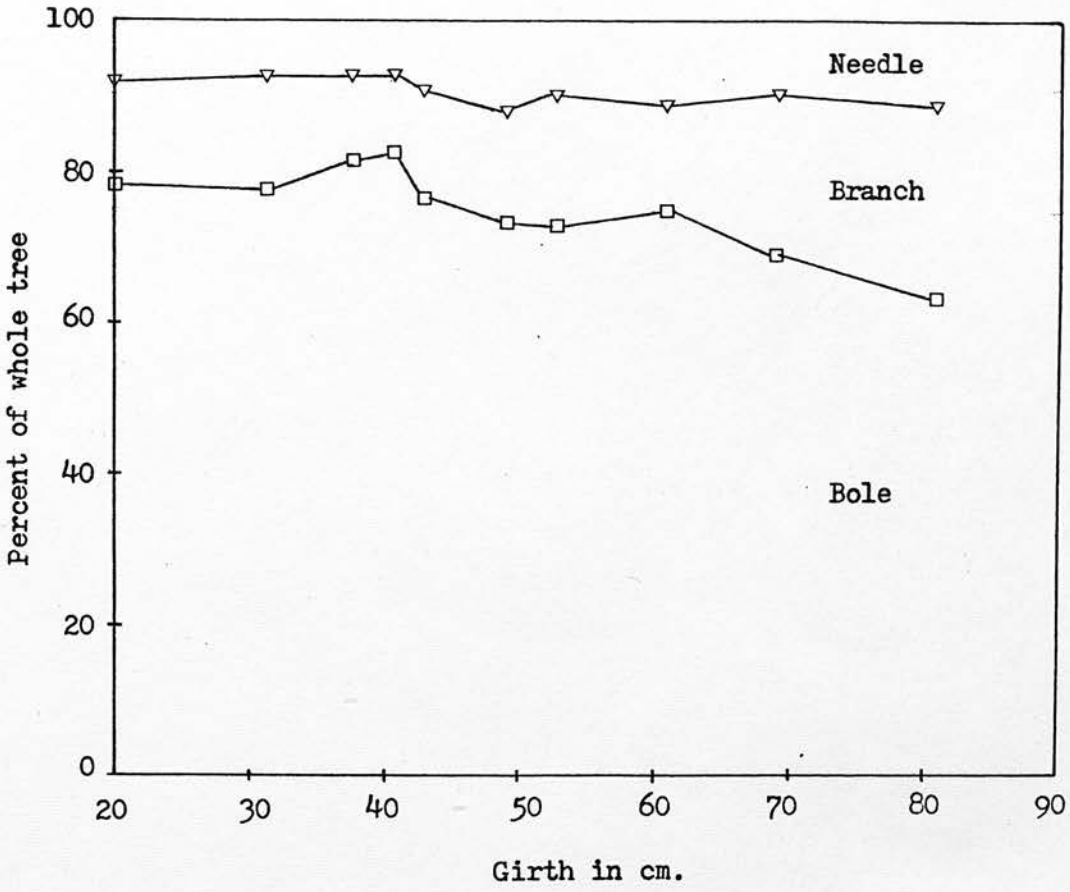

Figure 1. Variation in the proportions of needles, branches and boles with girth size in the sample trees.

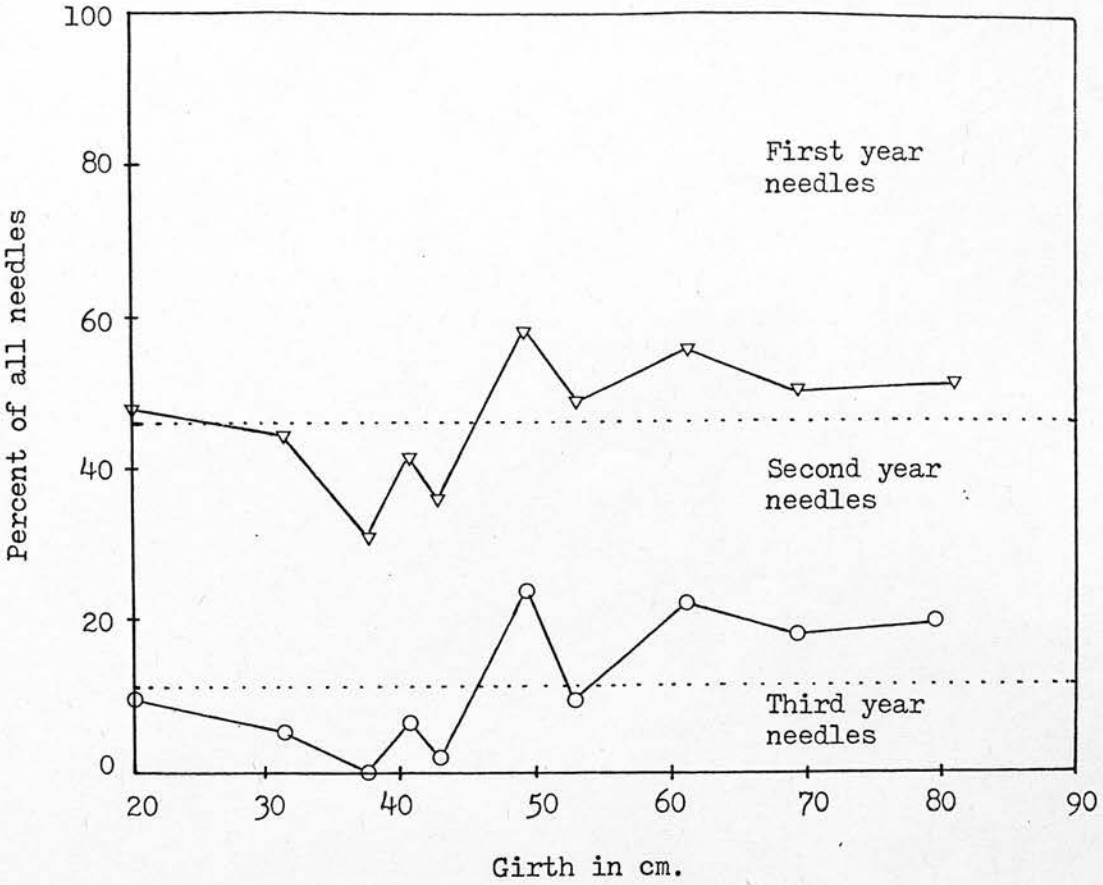

Figure 2. Variation in the proportions of first-, second- and third-year needles with girth size of the sample trees.

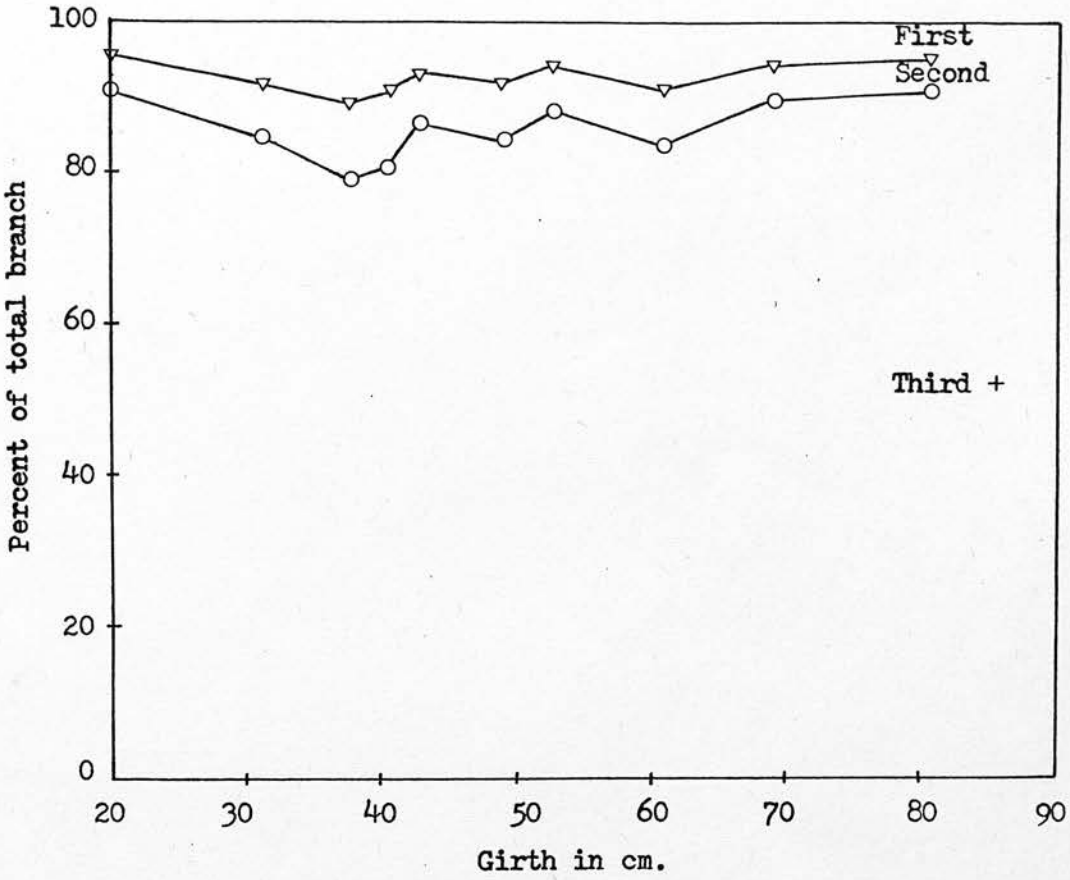

Figure 3. Variation in the proportions of first-, second- and third-and-over- year shoots and branches with girth size in the sample trees.

of these 4-year old needles also seems to be related to the amount of sunlight present as they are found mainly on the more exposed shoots and branches of the bigger trees.

3.3.3.3. Bole Components

The bark constitutes an average of 8.9% of the bole and this proportion does not vary much with tree size (Figure 4). The three outer wood rings account for less than 10% of the total weight of the bole in the smallest sample tree. This low proportion is related to the very narrow outer rings in the stem and reflects the supressed status of the tree. In the bigger trees, these three outer rings make up over 15% of the total weight of the bole and the proportions of these and other wood rings in these trees do not show any trend with increasing tree size. The three outer wood rings each average between 6.6 and 7.3%, and the fourth to tenth ring and the inner core account for 31.6 and 38.7% respectively. Of the three outer wood rings, the middle one has the highest weight. This second year wood ring corresponds to the wood production in 1975, which , based on on-going measurements of girths, heights and litter production in an adjacent study plot, was the year of highest productivity since the last thinning in 1971 (Cousens, pers. comm.).

3.3.4. Correlations

Although the proportions of most of the components do not show any relationship with size of trees, the actual weights of most of them (Appendix Table II) are highly correlated with girth

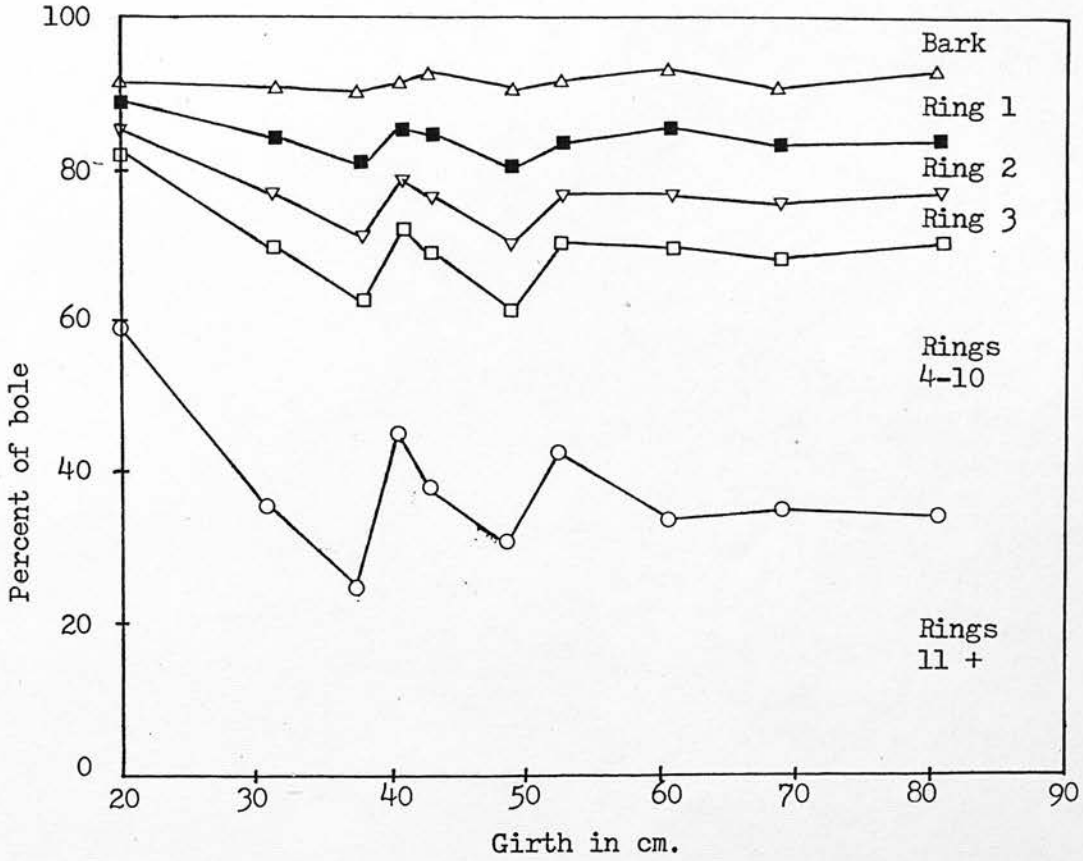

Figure 4. Variation in the proportions of bark and the various wood rings with girth size in the sample trees.

($r > 0.95$) (Table 3). Exceptions are the weights of dead branches (which was poorly correlated), the weights of third year needles (which was not correlated at all), and the weights of cones which occur only on some codominant and dominant trees.

3.4. Biomass in the Stand

3.4.1. Estimation

3.4.1.1. Tree Components

The weights of the different components of each tree in the six plots are estimated individually from their corresponding girths using the various regressions (from Table 3). Where the weights are not correlated with girth as in the case of cones, third year needles and dead branches, the biomass is obtained as the difference between estimates with and without that particular component. The weight of third year needles, for example, is obtained by subtracting the estimated weights of the first and second year needles from the estimated weight of all the needles. Where the weights are obtained from separate regression equations, the weights of the different components are not additive (Dice, 1970), that is, the sum of the weights of needles, branches and bole, each of which was determined from separate equations, is not equal to the total weight predicted by the equation which estimates the total weight of the tree. The difference arising out of this is, however, very low and is generally less than 1% of the total obtained by regression.

Table 3. Statistics of regressions relating weights of various components to girth in the form log (weight) = b.log (girth) + c. Regressions were based on 10 sample trees collected in 1977.

Component	b	c	r	$\bar{y}$ *	t	Correction factor
Total live above ground	2.3353	0.8726	0.9988	4.7355	58.52	1.00017
Total above ground (incl. dead branches)	2.2893	0.9811	0.9979	4.7681	43.58	1.00037
Total Bole (incl. bark)	2.1939	0.9810	0.9973	4.6101	38.20	1.00059
Live Crown	2.7227	-0.3825	0.9874	4.1213	17.62	1.00337
Dead Branches	1.5689	0.9591	0.7155	3.5542	2.90	N.D.
Total live branches	2.7680	-0.6616	0.9818	3.9167	14.63	1.00499
Total Needle	2.5271	-0.5018	0.9807	3.6780	14.18	1.00443
1^{st} Year Twigs	2.7550	-1.8024	0.9891	2.7543	18.98	1.002899
2^{nd} Year Twigs	2.5989	-1.5672	0.9900	2.7314	19.81	1.00472
3^{rd} Year and older branches	2.7849	-0.7533	0.9745	3.8508	12.28	1.007192
1^{st} Year Needle	2.3793	-0.5380	0.9884	3.3973	18.38	1.00229
2^{nd} Year Needle	2.3806	-0.7174	0.9711	3.2201	11.59	1.00596
3^{rd} Year Needle	-226.8952	417.5413	-0.3178	42.2596	0.95	N.D.

* corresponding $\bar{x}$ (=1.6540) is the same for all components since the x variable is log (girth).

Table 3. continued

Component	b	c	r	$\bar{y}$	t	Correction factor
Cones	4.7362	-7.1288	0.5134	0.7056	1.69	N.D.
Bark	2.1463	0.0066	0.9898	3.5569	19.63	1.00166
Wood	2.1994	0.9324	0.9971	4.5706	36.87	1.00048
1^{st} Year Wood Ring	2.7104	-1.0480	0.9688	3.4355	11.05	1.00848
2^{nd} Year Wood Ring	2.6585	-0.9399	0.9593	3.4577	9.60	1.01079
3^{rd} Year Wood Ring	2.6028	-0.8880	0.9641	3.4174	10.27	1.00902
4 - 10^{th} Year Wood Rings	2.4025	0.1316	0.9898	4.1058	19.68	1.00207
11^{th} Year and older rings	1.9416	0.9771	0.9742	4.1887	12.22	1.00353

b - regression coefficient

c - constant

r - correlation coefficient

$\bar{y}$ - mean of log (weight)

t - Student's t-value

$t_{0.05} = 2.31$

$t_{0.01} = 3.36$

N.D. - not determined as corresponding r values are low

3.4.1.2. Plot Estimation

The total biomass of each component in each plot was then obtained by summing all the individual estimates for that component in the plot and the results were converted to a per hectare basis. These estimates of biomass of the trees and tree components are not corrected for the bias arising out of detransforming the data since the correction factors, which are based on the error variance of the regression coefficients, are very close to 1.00 and the amounts of correction involved are all less than 1.0%.

3.4.1.3. Errors

The standard errors of the sampled means (Sokal and Rohlf, 1971) of the various major components (Table 2) and the standard errors of the mean biomass of the same components in the plots(Table 4) are all below 10% of their mean values. Except for the total tree estimate, the coefficients of variation of the means calculated on a plot basis are approximately half those calculated for the mean individual sample tree. This shows that although the regressions may not predict individual weights as accurately, they do give fairly reliable estimates on a stand basis. This is because, with a sufficiently large number of trees, the over-estimates and underestimates tend to cancel each other (Dice, 1970).

3.4.2. Biomass in Stands

3.4.2.1. Total Tree

The mean total above-ground biomass of the trees based on the

Table 4. Biomass of major components in the various plots (t/ha).

Plots	Needle	Branch	Cone	Bole	Total	Dead Branch
1977						
C1	10.10	18.25	0.62	81.97	111.75	7.82
C2	12.81	24.02	1.03	98.65	137.50	8.57
T1	11.49	21.32	0.86	90.02	124.55	8.08
T2	11.49	21.57	0.93	88.40	123.27	7.66
T3	11.25	21.14	0.92	86.36	120.58	7.45
T4	9.78	17.90	0.66	78.21	107.26	7.28
Mean	11.15	20.70	0.84	87.27	120.82	7.81
SE.	0.45	0.94	0.07	2.88	4.34	0.19
CV (%)*	4.0	4.5	7.9	3.3	3.6	2.4
1978						
C1	10.46	19.01	0.67	84.20	115.19	7.93
C2	13.29	25.06	1.11	101.56	142.03	8.69
T1	12.00	22.39	0.93	93.28	129.49	8.24
T2	11.98	22.58	0.99	91.76	128.22	7.88
T3	11.65	22.01	0.98	88.66	124.22	7.52
T4	10.18	18.76	0.72	81.20	111.76	7.44

* CV : Coefficient of Variation

biomass in the six plots is 120.82 t/ha (Table 4). This is made up of 11.2 t needles, 20.7 t branches, 87.3 t bole and 0.8 t cones. The total above-ground biomass of the trees in Devilla is generally comparable with values reported for other Scots pine stands elsewhere in Britain, although the biomass of the crown is somewhat higher, while the biomass of the bole is slightly lower than the corresponding obtained in other stands (Table 5). This higher crown to bole ratio as mentioned before, is related to the early opening of the canopy space brought about by the deaths of many trees during the first twelve years after planting.

3.4.2.2. Foliage

The stand contains an average of 5.6 t first year needles, 3.7 t second year needles and 1.8 t third year needles in each hectare (Table 6). The biomass of the different aged needles remains approximately the same in 1978 as the same regressions are used.

3.4.2.3. Branches

The biomass of branches in 1977 consists of 1.4 t first year shoots, 1.3 t second year shoots and 18.0 t third year and older branches (Table 7). This distribution of shoots and branches, however, does not represent the true age class distribution of tissues in the branches since the older branches contain current or 1-year and 2-year tissues as lateral growth as well. In order to obtain a more reasonable estimate of the first year and second year tissues, the exponential growth

Table 5. Biomass of needles, branch and bole in mature Scots pine stands.

Age (yrs)	Density (no./ha)	Biomass (t/ha) Needle	Branch	Bole	Total	Reference
32	4800	7.8	14.8	121.2	183.4	Attiwill & Ovington (1968)
35	1890	9.8	9.6	98.8	119.0	Ovington (1957b)
45	1420	4.4	7.4	60.9	72.7	Malkonen (1975)
47	845	3.5	6.8	30.4	40.8	Malkonen (1975)
47	445	27.0		129.6	156.6	Ovington (1956)
55	760	7.2	12.3	96.7	116.7	Ovington (1957b)
64	815	4.7	16.7	97.4	118.8	Wright & Will (1958)
46	1583	11.2	20.7	87.3	120.8	this study

Table 6. Biomass of different aged needles in 1977 and 1978 (t/ha).

Year	1977			1978		
Plots	First	Second	Third	First	Second	Third
C1	5.17	3.44	1.50	5.33	3.55	1.58
C2	6.40	4.26	2.14	6.62	4.40	2.26
T1	5.79	3.85	1.86	6.02	4.01	1.97
T2	5.74	3.82	1.93	5.98	3.98	2.03
T3	5.62	3.74	1.90	5.79	3.85	2.00
T4	4.97	3.31	1.51	5.15	3.42	1.61
Mean	5.62	3.74	1.81			

Table 7. Biomass of different aged branches in 1977 and 1978 (t/ha).

Year	1977			1978		
Plots	First	Second	Third	First	Second	Third
C1	1.25	1.16	15.81	1.30	1.20	16.47
C2	1.65	1.48	20.86	1.72	1.54	21.77
T1	1.46	1.32	18.50	1.54	1.39	19.44
T2	1.48	1.33	18.73	1.55	1.39	19.61
T3	1.45	1.30	18.36	1.51	1.35	19.12
T4	1.23	1.12	15.52	1.29	1.17	16.27
Mean	1.42	1.28	17.96			

model (Whittaker, 1965 ; Weaver, 1976) was applied to the branch weight data of the sample whorls in each of the ten sample trees. The model has the equation :-

$$\log (\text{weight}) = a + k.\log (\text{age})$$

where k is the growth constant, and the age of the whorl is assumed equal to the whorl number from the top of the crown.

For each whorl, the current annual increment is calculated as follows,

$$\text{increment } (y) = \text{weight of branch in whorl } (y) \times \frac{k}{\text{age of whorl } (t)}.$$

After summing the current annual increments from all the living whorls in a tree, the proportion of annual increment to the total weight of branch was calculated. Based on the ten sample trees, the current annual increment accounted for 15.37% of the total weight of branch. The estimates of the current annual production of branch biomass in the plots were obtained by multiplying the total branch biomass in each of the plots by 0.1537 and the weights of the second year tissues were also estimated assuming that they made up 15.37% of the remaining second year and older tissues (Table 8).

3.4.2.4. Bole

The total biomass of the bole in 1977 consists of an average of 7.6 t of bark, 6.7 t first year wood, 7.0 t second year wood, 6.2 t third year wood, 28.8 t fourth to tenth year wood and 31.1 t of wood over 10 years old (Table 9a).
The regressions could also be used with the 1978 girth data to obtain similar distributions of bark and wood rings in 1978.

Table 8. Biomass of different aged tissues in branches in 1977 and 1978 predicted from growth model (t/ha).

Year	1977			1978		
Plots	First	Second	Third	First	Second	Third
C1	2.81	2.37	13.07	2.92	2.47	13.61
C2	3.69	3.13	17.21	3.85	3.26	17.95
T1	3.28	2.77	15.27	3.44	2.91	16.04
T2	3.32	2.81	15.45	3.47	2.94	16.17
T3	3.25	2.75	15.14	3.38	2.86	15.76
T4	3.06	2.59	14.25	2.88	2.44	13.44
Mean	3.24	2.74	15.06			

Table 9. Biomass of bark and various wood rings in the bole in a) 1977 and b) 1978 (t/ha).

a) 1977

Plots	Bark	Ring 1	Ring 2	Ring 3	Ring 4 - 10	Ring 11+
C1	7.20	5.96	6.22	5.61	26.48	30.05
C2	8.61	7.77	8.04	7.20	32.93	34.76
T1	7.87	6.91	7.17	6.43	29.72	32.16
T2	7.71	6.98	7.22	6.46	29.53	31.12
T3	7.53	6.84	7.07	6.33	28.90	30.31
T4	6.86	5.83	6.06	5.46	25.50	28.41
Mean	7.63	6.72	6.96	6.25	28.84	31.14

b) 1978

Plots	Bark *	Ring 1 *	Ring 2	Ring 3	Ring 4 - 11	Ring 12+
C1	7.39	6.20	5.93	6.19	31.90	29.77
C2	8.85	8.10	7.74	8.00	39.92	34.48
T1	8.15	7.25	6.87	7.13	35.93	31.92
T2	8.00	7.30	6.97	7.21	35.95	31.05
T3	7.72	7.11	6.77	7.00	34.82	29.86
T4	7.05	6.13	5.78	6.01	30.69	27.98

* Estimated using regressions on 1978 girth data.

Other rings estimated from 1977 estimates minus mortality.

However, if this was done, the biomass of the second year and older wood rings obtained (for 1978) would be much lower than the biomass of wood in 1977 than could be accounted for by death and other losses. Instead, only biomasses of the bark and the first year wood ring are estimated from the 1978 girth data using the regressions, while the biomass of the other wood rings are obtained from the 1977 data by subtracting losses due mainly to death of trees (Table 9b). As the second year rings in 1978 were first year rings in 1977, the total biomass of the second year ring in 1978 is equal to the biomass of the first year ring in 1977 minus the appropriate losses. The biomass of the third year wood ring in 1978 is also estimated in a similar way from the biomass of the second year wood in 1977. To simplify calculations the biomass of the third year ring in 1977 is added to that of the fourth to tenth year rings in 1977 and then adjusted for loss to give the biomass of a fourth to eleventh ring band in 1978, while the biomass of the inner core in 1978, consisting of wood over eleven years old, is equal to the biomass of the same core in 1977 minus the loss through death.

3.5. Biomass Increment

3.5.1. Total Annual Production

3.5.1.1. Estimation

An estimate of the total annual production, excluding amounts used in respiration, can be obtained by summing the biomass of all the first-year tissues. As the samples were

collected in March 1977, the value obtained would represent the production during the summer of 1976. The large cones have been included in the estimates for total production even though they are two years old, since their biomass accrues mainly in their second year. As the bark was not subdivided into age classes due to practical difficulties in recognising tissues of different age, the annual production of the bark of the bole has been estimated by multiplying the total weight of bark with the ratio of the biomass of the current year wood ring to the total biomass of the wood.

3.5.1.2. Total Amount

An average of 17.0 t of organic matter was produced in each hectare (Table 10). This is higher than the value obtained from the production curves of Ovington (1959a) for a similarly aged stand of Scots pine but is comparable with the production of somewhat younger stands. This perhaps further supports the recommendation of Hamilton and Christie (1971) that the period of restricted growth should be discounted in the assessment of yield class of the stand. The total annual production of the bole and branch fractions are also comparable with the bole and branch production predicted for younger stands, but the total annual production of needles is much higher than the maximum predicted from the data of Ovington (1959a).

Table 10. Total annual production based on weights of current year tissues in 1977 and 1978 (t/ha)

Plots	Needle	Branch	Cone	Bole		Total
				Wood	Bark	
1977						
C1	5.17	2.81	0.62	5.96	0.61	15.17
C2	6.40	3.69	1.03	7.77	0.72	19.61
T1	5.79	3.28	0.86	6.91	0.66	17.50
T2	5.74	3.32	0.93	6.98	0.65	17.62
T3	5.62	3.25	0.92	6.84	0.63	17.26
T4	4.97	3.06	0.66	5.84	0.58	15.10
Mean	5.62	3.24	0.84	6.72	0.64	17.04
1978						
C1	5.33	2.92	0.67	6.20	0.62	15.74
C2	6.62	3.85	1.11	8.10	0.74	20.42
T1	6.02	3.44	0.93	7.25	0.68	18.32
T2	5.98	3.47	0.99	7.30	0.67	18.41
T3	5.79	3.38	0.98	7.11	0.65	17.91
T4	5.15	2.88	0.72	6.10	0.59	15.44

3.5.2. Net Accumulation

3.5.2.1. Crown

Not all of the gross annual production is, however, retained since there are losses through litter production and death of the large branches as well as some tree mortality. In a mature stand in which the canopy is no longer open, the biomass of the needles and branches would tend to remain fairly constant. A high total annual production is balanced by high turnover. Based on the total biomass of needles and branches in 1977 and 1978, there are small net accumulations of needles and branches (Table 11). While this is a result of using the larger girth values obtained in 1978 with the regressions, it may also indicate that crown closure is not quite complete.

3.5.2.2. Bole

The biomass of the bole, unlike that of the crown components, is not limited by the available canopy space and so can continue to increase. The only losses are in the mortality of some supressed trees and the flaking off of small amounts of stem bark. As these losses are very low, a very large proportion of the gross annual production is retained. The accumulation in the bole wood is thus estimated as equivalent to the biomass of the first year wood ring (Table 11). The net accumulation of the bark, based on the total bark biomass in 1977 and 1978, varied between 0.19 and 0.29 t/ha.

Table 11. Annual accumulation of biomass in Devilla from 1977 to 1978 (t/ha).

Components	Plots					
	C1	C2	T1	T2	T3	T4
Needles	0.36	0.48	0.51	0.50	0.38	0.40
Branch	0.75	1.04	1.08	1.01	0.87	0.86
Bole Bark	0.14	0.24	0.28	0.29	0.19	0.19
Wood	6.20	8.10	7.25	7.30	7.11	6.10
Total	7.45	9.86	9.12	9.10	8.45	7.55
- Mortality	0.73	0.80	0.79	0.19	1.45	1.16
Net	6.72	9.06	8.33	8.91	7.00	6.39
Mean	7.89		8.62		6.70	

3.5.2.3. Total

After taking into consideration all the losses that occured during the year, the total net annual accumulation varied between 6.4 and 9.1 t/ha (Table 11). This amounts to slightly less than half the total annual production, and is comparable with the value of 47% estimated for a 36-year old Douglas fir stand in North-West America (Dice, 1970).

CHAPTER 4.

RESULTS AND DISCUSSION II. DISTRIBUTION OF NUTRIENTS IN THE STAND

4.1. Introduction

As information on the distribution of various nutrients is essential for the study of nutrient cycling, the concentrations of the relevant nutrients have to be determined accurately. In this chapter, the method used will be discussed, followed by the results on the concentrations of nutrients in the various components and the changes in these concentrations with age. The next section deals with the nutrient capital in the above-ground parts of the trees in the stand, while the final section deals with the requirements for annual production.

4.2. Sampling Method

As needles, branches and boles are different anatomically and physiologically, they have to be analysed separately so that variations due to morphological differences of the components are minimised (Rennie, 1966). To demonstrate and estimate retranslocation in the different components further requires that these components be subdivided into different age classes. Hence, 13 live component fractions, consisting of three age-classes each of needles and branches, five of bole wood, one each of bole bark and cones, and one dead branch fraction were adopted for separate analysis.

The subdivision of needles and branches into different age classes for analyses is widely used, mainly to improve the estimates of content (Wright and Will, 1958; Ovington, 1959a; Malkonen, 1974 and Lehtonen, 1978 working on Scots pine; Wells and Metz, 1963; Baker, Switzer and Nelson, 1974; Webber, 1977 and Turner,1977 working on other conifers). Subdividing the bole wood into rings of different ages on the other hand is a less common procedure (Wright and Will, 1958; Turner, 1977) as bole wood samples are more commonly analysed as a complete disc or wedge sample (Malkonen, 1974; Young and Carpenter, 1976). Wright and Will (1958) subdivided their wood samples into two to five classes of approximately equal volumes but each containing a varying number of rings, while Turner (1977) analysed only the ten outermost rings separately and did not refer to any sample of the remaining core.

4.3. Concentration of Nutrients in Trees

To demonstrate the change in concentration with age more effectively, the mean concentrations of the different nutrients in 1977 in the various fractions are plotted against the age of the relevant component (Figures 5, 6 and 7). The actual values and their S.E.'s are tabulated in the Appendix (Table III).

4.3.1. Major Components

The highest concentrations of all the nutrients are found in the needle fraction, while the lowest are in the wood. This

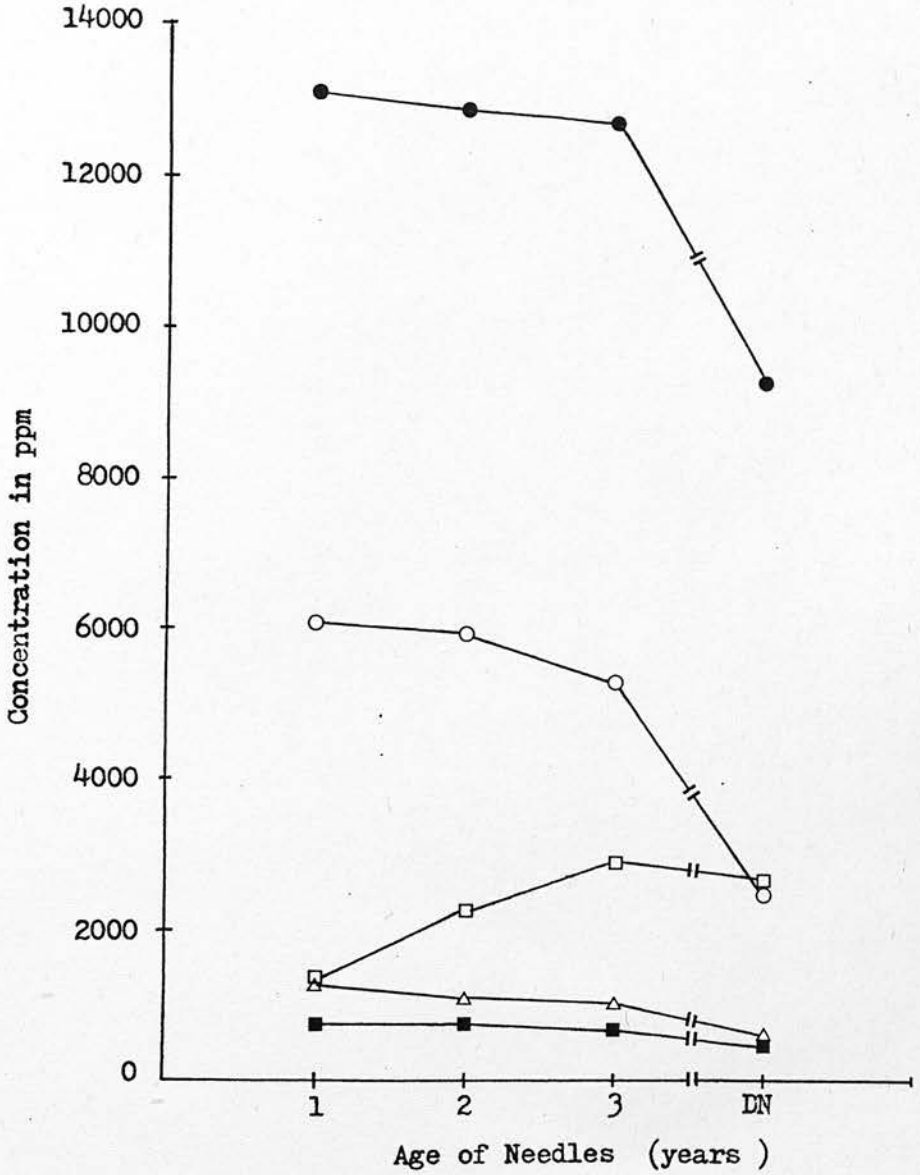

Figure 5. Concentrations of N (●), P (■), K (○), Ca (□) and Mg(△) in first-, second-, and third-year needles and dead needles (DN).

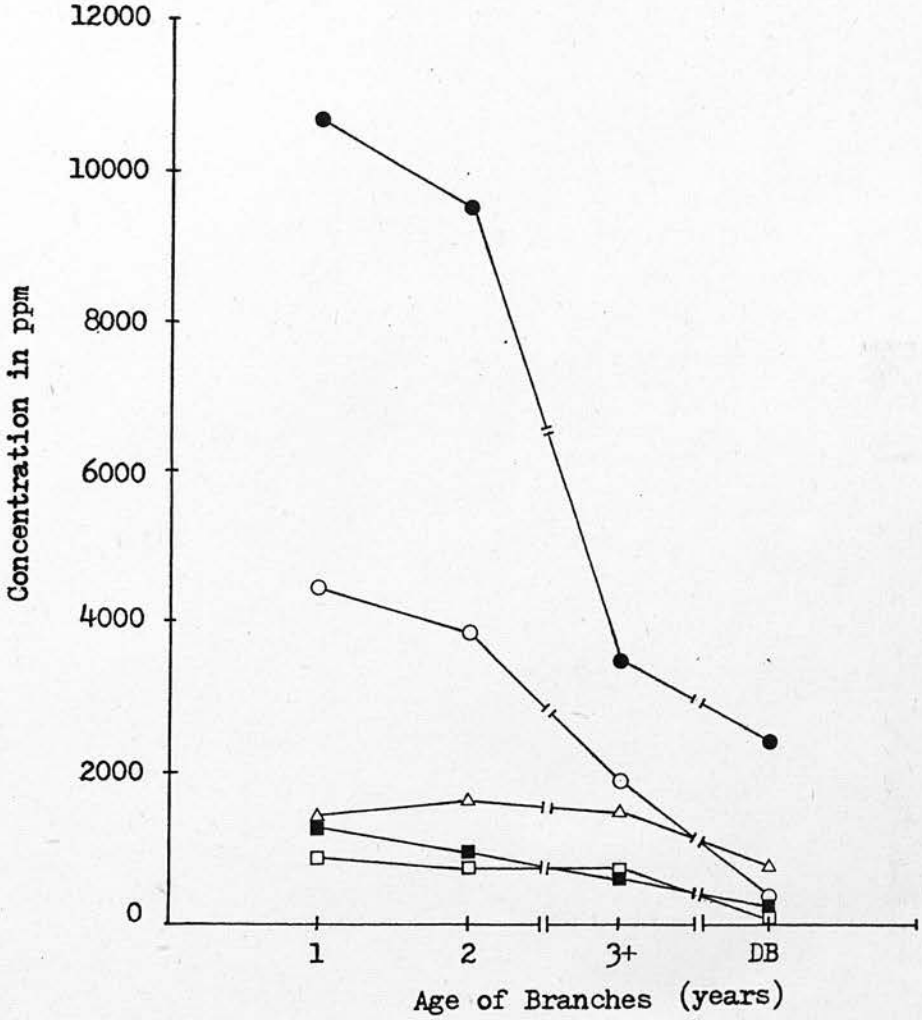

Figure 6. Concentrations of N (●), P (■), K (○), Ca (□) and Mg (△) in first-, second-, and third-year and over branches and dead branches (DB).

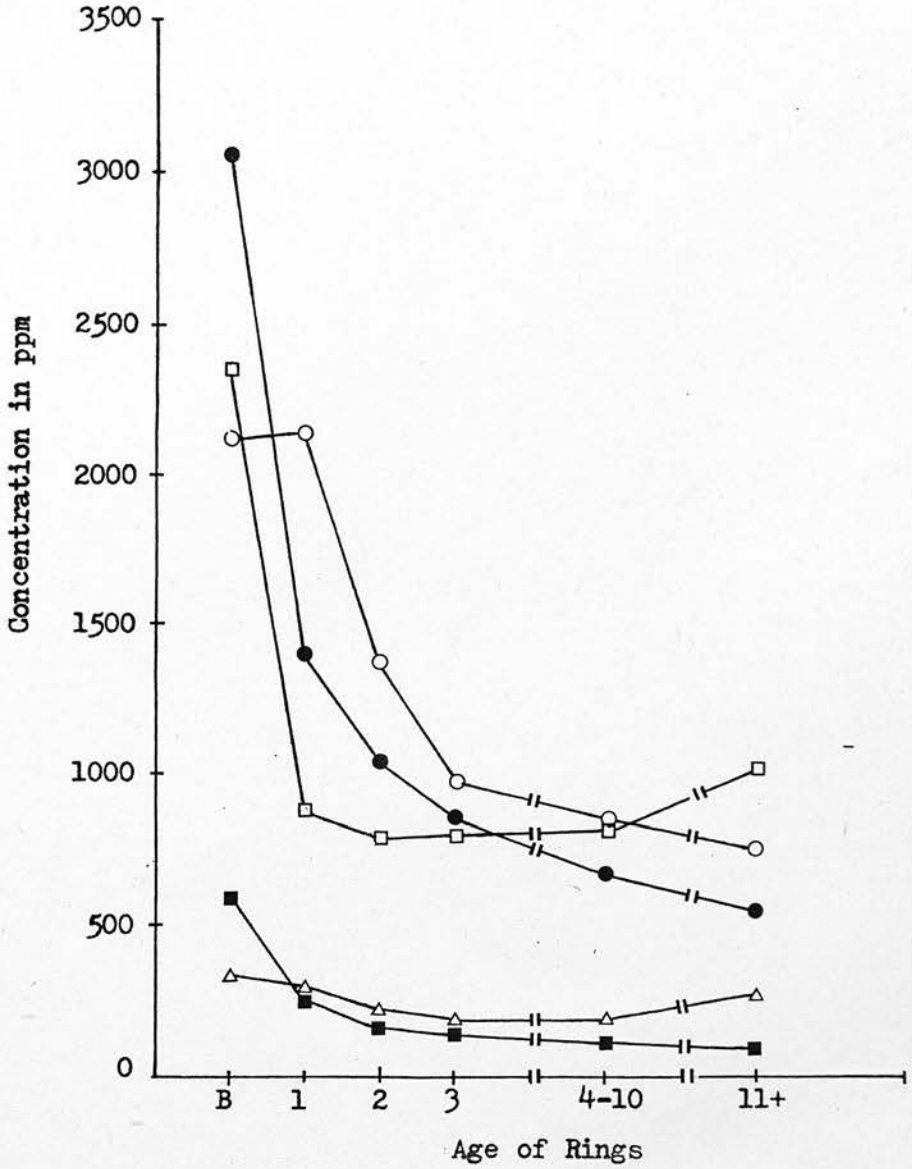

Figure 7. Concentrations of N (●), P (■), K (○), Ca (□) and Mg (△) in the bole bark (B) and wood rings of different ages.

is as expected, since needles are physiologically more active than wood and hence require more of these nutrients, all of which are essential for various biochemical and physiological processes. The presence of living and physiologically active tissues in the form of phloem also accounts for the relatively high concentrations of these nutrients in the bark as compared to the wood which consists mainly of dead cells (Epstein, 1971).

The concentrations of all the nutrients are generally comparable to other values reported for Scots pine (Wright and Will, 1958; Ovington, 1959a; Ovington and Madgwick, 1959; Malkonen, 1974) and other conifers (Wright and Will, 1958; Madgwick, 1964; Miller, 1966; Young and Guinn, 1966; Morrison, 1974; Young and Carpenter, 1976). The concentration of P and Ca, however, tend to be at the lower end of the range reported and this may be due to the low fertility of the underlying sandstone soils found in the area.

4.3.2. Changes with Age

The concentrations of N, P, K and Mg in all the three major components generally decrease with age of the component, while the concentration of Ca tends to increase with age (Figures 5 - 7). Analysis of variance (of the data from which the means are derived) reveals that most of these variations in concentration with age are significant, the exceptions being the concentrations of N and Mg in the needles and Ca in the branches and wood (Table 12).

A decline in concentration with age may result from the loss of nutrients through leaching and/or physiological withdrawal and

Table 12. Levels of significance in comparisons of concentrations of N,P,K,Ca and Mg in tissues of differnt age.(percent probability; NS - Not significant)

Components	N	P	K	Ca	Mg
Needles	NS	0.1	0.1	0.1	NS
Branches	0.1	0.1	0.1	NS	1.0
Wood	0.1	0.1	0.1	NS	1.0

Table 13. Mean content of N,P,K,Ca and Mg in various components (kg/ha). Values in brackets represents percentage contribution to total.

Component	N	P	K	Ca	Mg
Needle	144.8 (43.6)	12.9 (37.4)	65.8 (31.1)	20.7 (14.9)	9.5 (20.5)
Branch	84.2 (25.4)	8.5 (24.6)	45.3 (21.4)	30.2 (21.7)	8.1 (17.4)
Bole	100.7 (30.4)	12.9 (37.4)	99.6 (47.1)	87.7 (63.0)	28.7 (61.9)
Total	331.7	34.5	211.5	139.1	46.4
Dead Branch	18.9	2.0	2.4	5.8	0.5

redistribution as well as from dilution through increases in amounts of organic matter; while an increase in concentration with age can result from the accumulation of the nutrient or from 'concentration' caused by loss of other materials from the tissues. By careful consideration of the physiological and chemical properties of the element and the amounts involved in each of the processes of change, the importance of retranslocation and leaching may be assessed.

4.3.2.1. Needles

Although needles tend to continue increasing their dry weights as they mature (Malkonen, 1974), measurements of the mean dry weight per needle of first, second and third year needles did not show any such increase. This indicates that decreases in concentrations in needles are more likely to be due to losses from leaching and/or redistribution than to dilution from an increase in the organic matter content. The similar concentrations of N in all the needles in 1977 show that little or no N is lost from the needles while the somewhat higher concentration of N in the second year needles in 1978 suggests that N may be accumulated (Figure 5). The fall in concentration of P with age is due mainly to withdrawal and redistribution as losses through leaching are very low (see Chapter 6). The fall in concentration of K is also the result of withdrawal and redistribution as well as leaching since K is a very mobile and soluble ion and a considerable amount of K is lost through leaching. In contrast, the concentration of Ca in the needle increases with age mainly because Ca is

relatively immobile and as an important constituent of cell-walls, is not withdrawn and redistributed, but continuously accumulated instead. Similar increases in the concentration of Ca and decreases in concentration of P and K in needles with age have been reported previously in Scots pine needles (Wright and Will, 1958; Ovington, 1959a; Malkonen, 1974).

4.3.2.2. Branches

Because of practical difficulties in separating branches into tissues of different age classes, the concentration of N, P, K, Ca and Mg are based on age of shoots instead of the true age of tissues. The decrease in the concentration of N, P, K, and Mg with age (Figure 6) may be due to the higher content of wood and the relatively lower proportion of bark in the older branches as well as to leaching and retranslocation. The marked decrease in concentrations from the first to second year shoots, which are very similar in appearance, and probably in structure, suggests that nutrients are removed from the older tissues. This loss may occur through leaching and internal redistribution. Ovington (1959a) also found that concentrations of N, P and K decrease with increasing age of branches while Smith, Nelson and Switzer (1963) also noted a marked decrease in the concentration of N from the current year branches to older branches.

4.3.2.3. Wood

The decrease in concentration of N, P and K with age in the

stem-wood is most marked in the outer rings (Figure 7). As no leaching can occur, this change is due entirely to retranslocation. Dilution resulting from an increase in organic matter may occur, but is unlikely as new growth in the following year would form new first year rings rather than increase the organic matter content of older rings. The increase in the concentration of Ca with age could be due to accumulation of Ca as well as a 'concentration' effect resulting from the removal of the other nutrients. Wright and Will (1958) also found marked decreases in the concentrations of N, P and K and an increase in the concentration of Ca with increasing age of rings in Scots pine growing on sand dunes.

4.4. Nutrient Capital in the Stands

The needle fraction contains over 35% of all the N, P and K, 18% of Ca and 30% of Mg found in the above-ground parts of the trees, even though they account for approximately 8% of the organic matter (Table 13). In comparison, the bole which makes up about 75% of the dry weight contains only 28% of all the N, 32% of P, 38% of K, 61% of Ca and 30% of Mg. This difference in proportional content which results from the different physiological demands of the different components becomes important when the turnover of the various nutrients and the different components are considered. Whereas most of the nutrients in the bole are not available for recycling because of the continuous accumulation of wood and the low turnover of boles, most of the nutrients in the needles are

available for recycling as there is little or no net accumulation and the turnover of needles is rapid. Furthermore, the nutrients in the needles are subject to leaching by rainwater.

The living above-ground parts of the trees in the plots contain an average of 332 kg N, 35 kg P, 212 kg K, 139 kg Ca and 46 kg Mg per hectare. The amounts of N, P and K are higher than those reported for other mature Scots pine and other pines, but are comparable with the amounts found in mature Douglas fir stands in North-western America (Table 14). The higher content of these nutrients in Devilla Forest is partly a result of the relatively higher biomass of the crown in Devilla. Whereas the biomass of the crown accounts for less than 20% of the above-ground biomass in most other stands (Ovington, 1957b; Wright and Will, 1958; Ovington and Madgwick, 1959), it averages about 25% in Devilla. The higher density of the trees in Devilla compared with these other stands may also account for the higher amount of N, P and K in Devilla. Further the trees in Devilla are near the end of a thinning cycle so that the biomass and the nutrient content of the stand would be higher than in a stand which has just been thinned.

4.5. Nutrient Content in Annual Increment

4.5.1. Total Annual Production

The total amount of an element required for the total annual production is estimated by summing the contents of that nutrient in all the first year tissues (Table 15). The total obtained in

Table 14. Content of N, P, K, Ca and Mg in stands of Scots pine and other pines and Douglas fir (kg/ha).

Species	Age	N	P	K	Ca	Mg	Reference
Pinus sylvestris L.	33	265	30	170	194	39	Ovington & Madgwick (1959)
	35	307	28	180	204	47	Ovington (1959a)
	45	109	46	46	51		Malkonen (1974)
	47	150	15	73	100		Malkonen (1974)
	55	269	24	107	179	44	Ovington (1959a)
	64	183	20	89	180	31	Wright & Will (1958)
P. banksiana Lamb	30	165	14	82	112	18	Foster & Morrison (1976)
	50	160	20	75	65	20	MacLean & Wein (1977)
P. nigra var. calabrica Schneid.	48	165	20	119	140	34	Wright & Will (1958)
P. taeda L.	20	174	19	99	91	24	Switzer & Nelson (1972)
Pseudotsuga menziesii (Mirb.) Franco	20	185	31	102	196	23	Webber (1977)
	36	323	67	224	339	50	Dice (1970)
	49	333	61	201	356	52	Turner (1975)

Table 15. Amounts of N, P, K, Ca and Mg bound to the annual production in 1976 (kg/ha).

	N	P	K	Ca	Mg
Needle	73.6	7.2	32.5	7.4	4.8
Branch	27.5	3.2	12.1	4.4	2.6
Cone	1.1	0.1	0.7	0.5	0.1
Bole	13.0	2.3	16.8	8.5	2.4
Total	115.2	12.8	62.1	20.8	9.9

Table 16. Amounts of N, P, K, Ca and Mg accumulated annually (kg/ha).

	N	P	K	Ca	Mg
Needle	0.6	< 0.1	0.2	0.1	0.1
Branch	1.0	< 0.1	0.4	0.1	0.1
Bole	13.0	2.3	16.8	8.5	2.4
Total	14.5	2.4	17.4	8.7	2.6

this way probably underestimates the actual total requirement as the requirement for the production of the male cones, which make up a large fraction of the miscellaneous fraction in the litterfall, is not considered. Furthermore, the requirement for bark production is based on the mean concentration found in the bark, whereas the actual concentration of the current year tissues consisting mainly of phloem and cambium could be much higher.

These values are below the maximum current annual uptake (which is equivalent to the annual requirement in this study; but which is estimated in a different way) estimated for Scots pine and are generally more similar to the estimates for younger stands than stands of a similar age (Ovington, 1959a).

4.5.2. Net Accumulation

Not all of the nutrients in the annual production, however, are accumulated as there are losses, especially from the crown components. As with total production of organic matter, most of the accumulation is in the bole. Based on the mean annual accumulation in the control plots (Table 11), approximately 14.5 kg N, 2.4 kg P, 17.4 kg K, 8.7 kg Ca and 3.3 kg Mg are accumulated annually (Table 16). Except for slightly lower values of N and Ca, these values are comparable with those reported for Scots pine (Malkonen, 1974), but are generally higher than those estimated for other pines (Foster and Morrison, 1976; Switzer and Nelson, 1972).

CHAPTER 5.

RESULTS AND DISCUSSION III. TRANSFER OF ORGANIC MATTER AND NUTRIENTS IN THE STANDS

5.1. Introduction

Having determined the biomass and nutrient distribution in trees, and the annual production, nutrient budgets have to be established. To do this, losses and transfers have to be determined. In this chapter, the method used for estimating retranslocation and uptake is first described, followed by the estimation of leaching. The loss of nutrients through litter production is discussed next and this is followed by the determination of retranslocation and uptake. The final section deals with the overall nutrient budget for Devilla.

5.2. Estimation

A diagram showing the distribution and transfers that occur from one year to the next can be used to establish some relevant equations of balance (Figure 8). The nutrients required for annual production (R) come from the soil by uptake (U) through the roots as well as from within the trees through the process of withdrawal and retranslocation (T). These three quantities are related as follows,

$$R = T + U \qquad (1)$$

R is equal to the content of the nutrient in the current year's tissues, while T is estimated from the change in the total

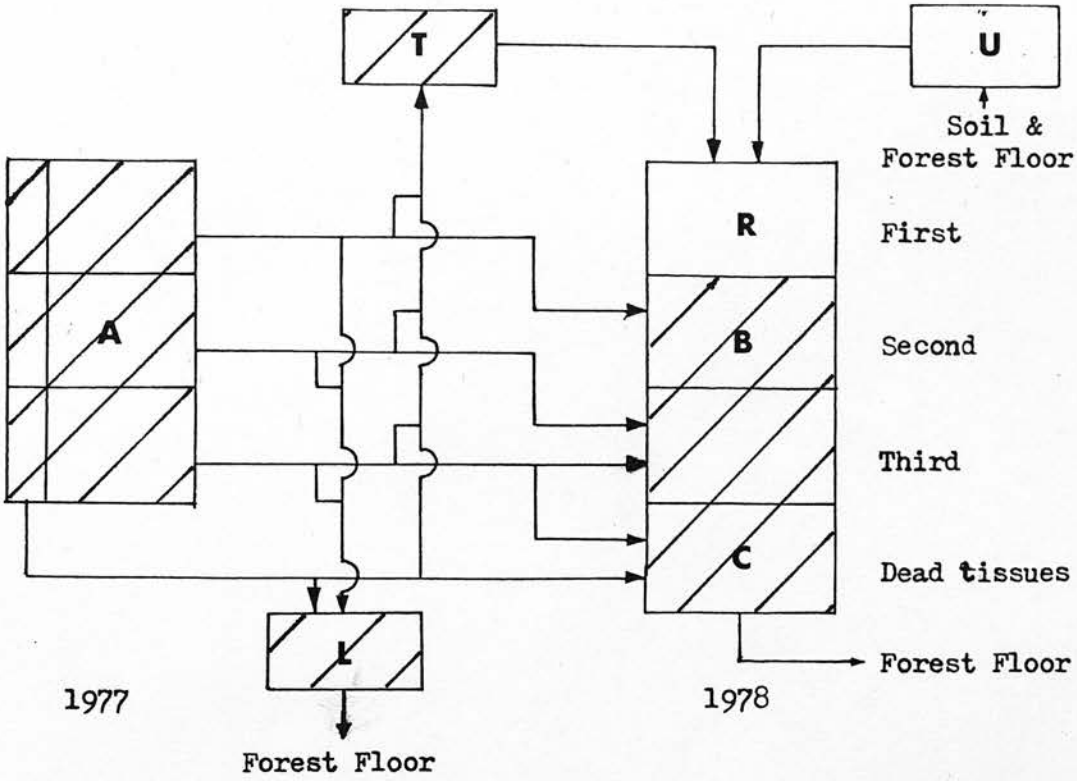

Figure 8. Diagram showing the flow of nutrients between different aged components from 1977 to 1978.

T = Retranslocation

U = Uptake

R = Requirement

A = Total amount in all living tissues in 1977

B = Total amount in 2nd. year and older living tissues in 1978

C = Total amount in tissues which died during the year

L = Total amount leached

content of a nutrient in a component over one year; the content in the second year includes the amounts lost through leaching and death, but excludes the new current growth (R). Following the notation in the diagram, the amount retranslocated from the tissue concerned is obtained as follows,

$$T = A - B - C - L \qquad (2).$$

The items involved in this balance are shaded in Figure 8.

Losses in the needle fraction through death are equal to the amounts in the needle litter produced, but losses in the branch and bole fractions are estimated from the changes in the biomasses of dead branches and of the boles in the trees which died between 1977 and 1978. Losses through leaching are estimated from inputs in the throughfall and to simplify the calculations, leaching is assumed to take place only from the needles. Losses through leaching from the branch fraction are included in the estimates for the needle fraction, so that for the determination of the amounts retranslocated from the branch and bole, the leaching term (L) in equation (2) is ignored.

5.3. Rainfall, throughfall and leaching

Rainfall and throughfall are important processes in the cycling of nutrients in ecosystems as the nutrients they contain represent additions to the pool of nutrients already within the system. Further, the amounts of some of the nutrients involved are high (Norton and Young, 1976; Henderson *et al.*, 1977; Swank and Henderson, 1976; Henderson and Todd, 1972; Carlisle, Brown and White, 1967 and Madgwick and Ovington, 1959). Nutrients in

the incoming rain are derived from dust, aerosols and other gaseous atmospheric pollutants and also from sea-sprays, while nutrients in the throughfall solution include contributions from the foliage and leaf-surface organisms through leaching as well as aerosols and dust particles within the canopy.

5.3.1. Rainfall and Throughfall

5.3.1.1. Amounts

The four-weekly rainfall varies quite considerably throughout the year (Figure 9). In summer there is a relatively dry period with less than 5cm of rain on each of four consecutive sampling occasions. In order to minimise errors that may arise from slightly earlier or later periods of high rainfall, the annual rainfall is based on collections from June of one year to June of the following year. The annual rainfall of 88cm agrees well with that predicted from the rainfall map prepared by the Meteorological Office, of between 85 and 90cm. This close agreement with the predicted values and the low coefficient of variation (<1.0%) suggest that the collecting funnels are sufficiently accurate and reliable in estimating the rainfall and throughfall.

The mean throughfall based on a total of 18 funnels from all the plots varies between 40 and 68% of the four-weekly rainfall and the annual throughfall based on these means is 52.4cm. This represents an overall throughfall percentage of 60% which agrees with values obtained for other conifer plantations

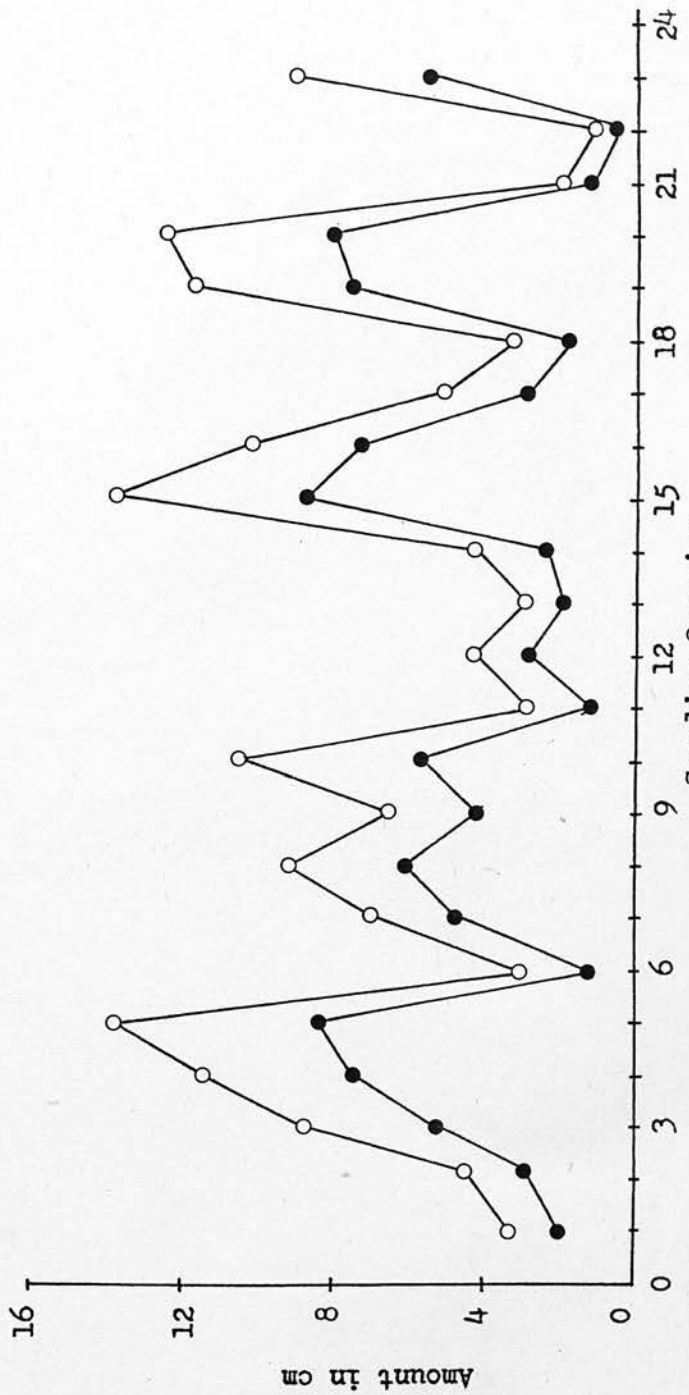

Figure 9. Four-weekly rainfall (○) and throughfall (●) in Devilla Forest from 23/6/77. Dates corresponding to the different sampling occasions are listed in the Appendix (Table V).

(Zinke, 1966; Miller, Cooper and Miller, 1976 and Gash and Stewart, 1977).

Stemflow was not measured, even though it may sometimes contain higher concentrations of some nutrients than throughfall (Miller, Cooper and Miller, 1976; Malkonen, 1974), because the volumes involved are usually very low (Gash and Stewart, 1977; Malkonen, 1974). Further, the large number of samples required to cover the range of variation in size and status of the trees found in the plots was beyond the resources available for this study.

5.3.1.2. Nutrient Content

The concentrations of the various nutrients in the incoming rain vary quite considerably throughout the sampling period (Table 17). To compensate for the differences in volumes obtained on different sampling occasions, the mean values are volume-weighted. The mean concentrations of all the nutrients in the incoming rain are below 1 ppm and agree with results obtained elsewhere (Swank and Henderson, 1976; Henderson et al, 1977; Feller, 1977). The input of nutrients into the system from rain is also similar to those reported for other forests (Madgwick and Ovington, 1959; Carlisle, Brown and White, 1967; Henderson and Todd, 1972; Swank and Henderson, 1976).

The concentrations of nutrients in the throughfall also vary over a wide range (Table 18). The mean concentrations of N and P, however, are very similar to those in the incoming rain-water, whereas the concentration of K is about 10 times as high

Table 17. Concentration and content of N, P, K, Ca and Mg in incident rain.

	N	P	K	Ca	Mg
Concentration (ppm)					
Mean	0.29	0.04	0.49	0.86	0.16
Minimum	0.02	< 0.02	0.14	0.43	< 0.06
Maximum	1.30	0.13	2.19	2.72	0.76
Content (kg/ha/an)	1.62	0.37	4.64	8.17	1.62

Table 18. Concentration and content of N, P, K, Ca and Mg in throughfall in the different treatment plots.

	N	P	K	Ca	Mg
Control Plot					
Concentration					
mean (ppm)	0.52	0.07	5.55	3.00	0.92
minimum	0.06	< 0.02	1.74	1.21	0.48
maximum	4.32	0.39	18.00	5.72	2.96
Content (kg/ha/an)	2.05	0.46	29.16	15.56	5.15
Fertilised Plot					
Concentration					
mean (ppm)	0.47	0.06	5.31	2.32	0.81
minimum	0.04	< 0.02	2.11	1.28	0.56
maximum	1.89	0.27	14.75	6.03	2.61
Content (kg/ha/an)	1.37	0.36	27.29	12.32	4.57
Saw-dust treated Plot					
Concentration					
mean (ppm)	0.46	0.08	5.04	2.99	0.97
minimum	0.03	< 0.02	2.27	1.28	0.52
maximum	1.79	0.32	15.50	7.27	3.38
Content (kg/ha/an)	1.31	0.47	26.56	16.33	5.30

and those of Ca and Mg are about three times as high. Similar values have been reported for throughfall solutions in other forests (Madgwick and Ovington, 1959; Lehtonen, 1976 ; Henderson et al, 1977) and for the total amounts reaching the forest floor (Madgwick and Ovington, 1959; Foster and Morrison, 1976; Henderson et al, 1977).

5.3.2. Leaching

The increase in the concentrations of nutrients such as K, Ca and Mg in the rain-water as it passes through the canopy has sometimes been attributed only to leaching from the foliage and the amounts leached estimated by subtracting the amount in the incoming rain from the total in the throughfall solution (Turner and Singer, 1976; Turner, 1977). This however, overestimates the amounts involved as nutrients from leaf washing and dust and aerosols are not excluded from the estimates (Turner, 1975, 1977).

5.3.2.1. Estimation

Very few studies have been conducted to separate the contributions due to aerosols from those due to leaching. Particle traps have been used to estimate the inputs from aerosols and dust particles separately, but their use has been limited to periods of dry weather (White and Turner, 1970; Swank and Henderson, 1976; Rolfe, Akhtar and Arnold, 1977). The amounts of nutrients in the throughfall can also be partitioned into the amounts due to leaching and those resulting from aerosols by relating the total in the throughfall to the total

in the incoming rain (Miller, Cooper and Miller, 1976) according to the equation,

$$y = b.x + c$$

where y = amount in throughfall

x = amount in incoming rain

b and c are constants.

The slope of the regression, b, is the constant representing the change in the content of a nutrient in the rain-water as it passes through the canopy. If this slope equals 1.0, there is no change in this content, suggesting that there is no addition from aerosols and no uptake by the foliage or leaf-surface organisms, or more likely, that absorption equals aerosols input; if the slope has a value less than 1.0, there is a net reduction in the content, showing that there is a net uptake of the nutrient by the leaves or leaf-surface organisms; and if the value of the slope is greater than 1.0, there is an enrichment of the nutrient from aerosols, that is in excess of any absorption. The intercept of the y-axis, c, represents the amount present in the throughfall when the content in the incoming rain is zero and may be regarded as the amount derived from leaching (Miller, Cooper and Miller, 1976).

5.3.2.2. Regression

The value of b for K is high, indicating that the aerosol contribution to K content is high, while the values of b for Ca and Mg approximate to 1.0, showing that the addition to these nutrients in the rain-water from aerosols are very low (Table 19).

Table 19. Regression statistics of nutrient contents in throughfall in the incoming rainfall.

Nutrient	b	c *	r	Significance
Nitrogen	0.8073	0.0497	0.7730	0.1%
Phosphorus	0.4200	0.0172	0.3588	1.0
Potassium	4.1201	0.6688	0.6563	0.1
Calcium	1.0050	0.5310	0.5099	0.1
Magnesium	1.1953	0.2382	0.5650	0.1

* c is in kg/ha/4 weeks

Table 20. Inputs of various nutrients from aerosols and leaching (kg/ha/an)

	N	P	K	Ca	Mg
b x (amount in rain)	1.309	0.154	19.177	8.209	1.942
Aerosol contribution	-0.313	-0.213	14.537	0.041	0.317
Leaching					
Control	0.741	0.301	10.038	7.346	3.210
Fertilised Plot	0.065	0.203	8.169	4.116	2.629
Saw-dust treated	0.294	0.318	7.447	8.118	3.358
Mean	0.367	0.274	8.551	6.527	3.066

In contrast, the values for N and P are less than 1.0, indicating that there is a net decrease in the content of these two elements, which may result from a higher amount of absorption relative to the input from aerosols.

The high values of c in the regressions for K and Ca indicate that high amounts of K and Ca are leached from the canopy, while the low values of c for N and P show that very little of N and P are leached.

5.3.2.3. Amounts

As the values of c represent the amounts of nutrients leached (in kg/ha) during each four-week period, they may be multiplied by 13 to give the amounts leached annually. Estimating the amounts leached by this method would, however, result in values of inputs from aerosols in the different treatment plots which vary quite considerably. Since such variations are not likely to occur within an area as small as the study area, the changes due to aerosols are instead first estimated from the slopes of the regressions by multiplying the slope, b, with the total amount in the incident rain.

The amounts leached are then obtained by subtracting these values from the separate treatment throughfall values (Table 20). The actual amounts contributed by aerosols (and absorption) are obtained by subtracting these same values from the amounts in the incoming rain.

The negative aerosol contributions of N and P suggest that there is a net absorption of these two elements in the canopy.

The aerosol contribution of K amounted to 14.5kg/ha/an, while additions of Ca and Mg were below 1.0kg/ha/an. Very low amounts of N and P were leached whereas over 10.0kg K was removed by leaching from the canopy.

5.4. Litter Production

5.4.1. Introduction

The production of litter is another important process whereby nutrients are returned to the soil (including the litter layer and humus complex) and recycled. Information on the amounts of organic matter and nutrients involved are essential for drawing up the nutrient budget of ecosystems. Under certain conditions, such as are found in stable climax forest stands, estimates of litter production are also useful as indices of productivity (Olson, 1963; Bray and Gorham, 1964).

5.4.2. Estimation

Although the collection funnels used were relatively small, the estimates of mean litter production are sufficiently reliable (Table 21). The mean needle and total litter production have standard errors which are less than 7% of their values and they are also statistically similar to estimates based on larger funnels (collection area of 0.25m^2) from an adjacent study plot (Cousens, unpublished data). Most of the litter falls between August and November while very little is produced between February and May (Figure 10).

Table 21. Production of needle and total litter in Devilla Forest (t/ha/an)
Values in brackets represent percentage contribution to total litter.

1977 - 1978	Control	Fertilised	Saw-dust
Needle	3.50 (78.2)	3.17 (70.4)	3.64 (70.5)
S.E.	0.26	0.13	0.19
Total	4.47 (100.0)	4.50 (100.0)	5.16 (100.0)
S.E.	0.27	0.54	0.37
1978 - 1979			
Needle	3.43 (75.1)	3.71 (72.1)	3.55 (74.6)
S.E.	0.15	0.22	0.15
Total	4.57 (100.0)	5.17 (100.0)	4.76 (100.0)

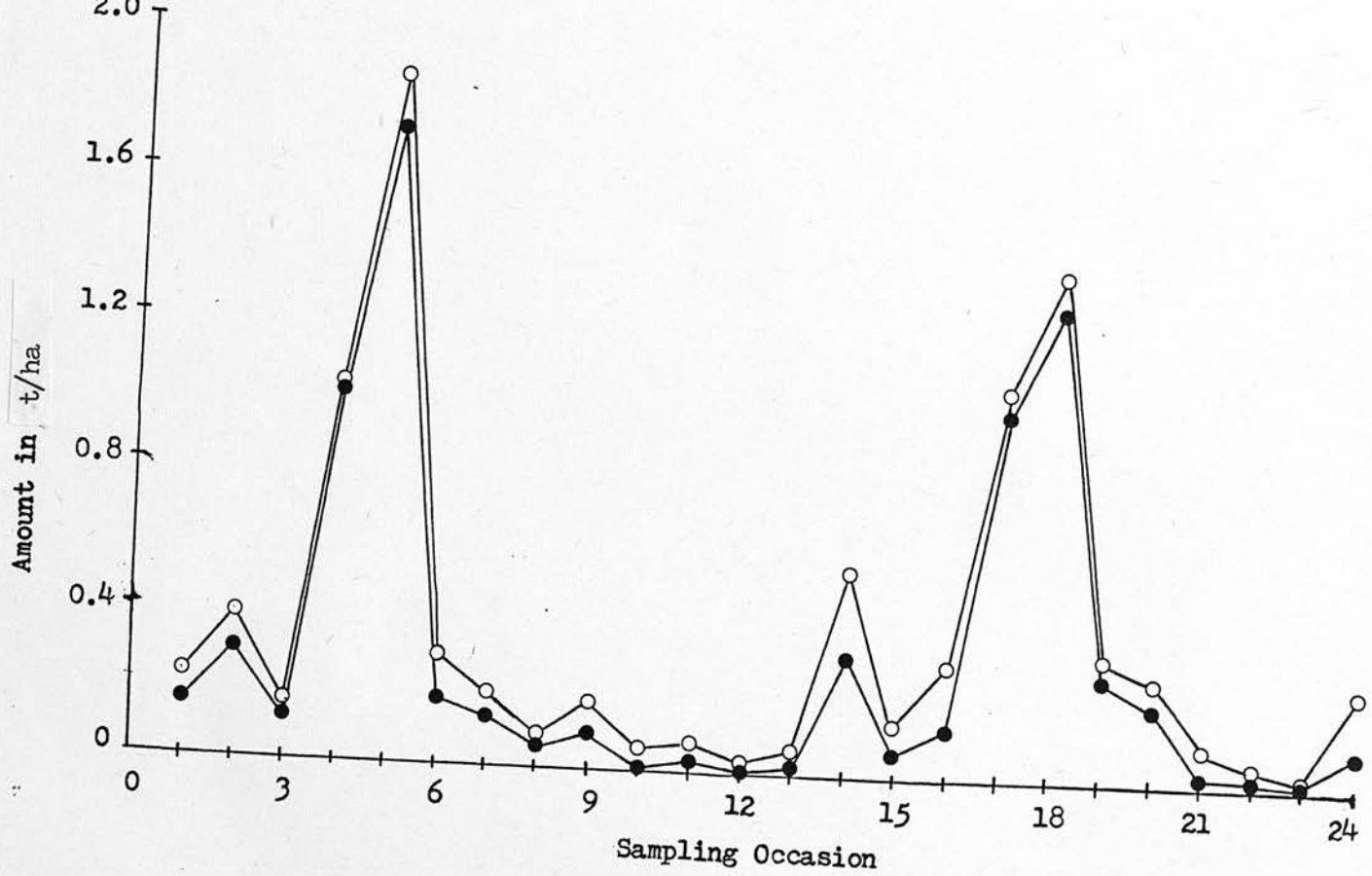

Figure 10. Four-weekly production of total (○) and needle (●) litter from 26/5/77 . Dates corresponding to the different sampling occasions are listed in the Appendix (Table VI).

5.4.3. Total Litter

Approximately 4.5 t of fine litter fall to the ground annually (Table 21). This value is within the range reported for pine forests but tends to be slightly higher compared to other Scots pine stands (Bray and Gorham, 1964; Carlisle and Brown, 1968; Lehtonen, 1978; Malkonen, 1974; Miller and Miller, 1967). The total litter consists of 78% needles, 4% twigs, 5% cones and 13% of miscellanea which is made up largely of bark, male cones and lichens.

5.4.4. Nutrient Content

The concentrations of most of the nutrients in the needle litter are generally lower than those in the live needles (Table 22; Figure 5) . The lower values of N, P and K result from their withdrawal and redistribution prior to falling and in the case of K to leaching as well. The concentration of Ca remains fairly constant as there is no loss due to redistribution. The concentration of most of the nutrients in the cone and twig fractions are low as these tissues contain a high proportion of wood; while the concentration of N in the miscellaneous fraction is high because of the inclusion of dead insects, frass and algae and lichens. Although the concentrations of N in the litter from fertilised trees are higher than those from the other trees, an analysis of variance shows that these concentrations are not significantly different with respect to treatments.

Table 22. Concentrations of N, P, K, Ca and Mg in various litter components (ppm).

Components	N	P	K	Ca	Mg
Control					
Needles	7320.0	523.1	1754.4	3256.7	512.9
Cones	2765.2	121.5	1155.8	436.1	99.5
Twigs	6923.9	211.0	894.0	1051.3	104.9
Miscellaneous	15599.6	563.9	1820.1	784.3	212.1
Fertilised Plots					
Needles	7431.1	509.7	1677.1	3095.7	521.7
Cones	3360.0	127.5	1029.2	418.2	115.5
Twigs	7656.3	271.2	872.8	1090.5	107.8
Miscellaneous	19243.0	672.2	2051.3	597.0	232.2
Saw-dust Treated Plots					
Needles	7131.2	491.3	1622.9	3277.6	513.5
Cones	3061.8	129.6	932.9	485.7	96.9
Twigs	7805.6	224.9	906.0	1065.4	106.3
Miscellaneous	15276.9	616.0	1822.1	737.7	137.3

Litterfall returned 36.6kg N, 2.2kg P, 7.6kg K, 12.1kg Ca and 2.0kg Mg to the soil. Of these, the needle fraction contributed up to 90% of the total for each element (Table 23). While the amounts of P, K, Ca and Mg are generally comparable with values reported for other pine stands (Bray and Gorham, 1964; Miller and Miller, 1967; Foster and Morrison, 1976) the amount of N is somewhat higher partly because of the relatively high contribution by the miscellaneous fraction.

5.5. Retranslocation and Uptake

5.5.1. Introduction

Using the data on nutrient distribution in 1977 and 1978 and losses during the intervening year, the amounts of each nutrient element retranslocated are estimated (Table 24). Separate nutrient budgets are established for each component in order to facilitate calculations as different components are associated with different losses and transfers, and to allow comparisons of the relative roles of retranslocation and uptake in the different components. The contribution which each source of nutrients makes to the total requirement can be assessed by relating the uptake or retranslocation to requirement. A high U/R ratio indicates that the soil-humus complex is the main source of the nutrient; while a high T/R or a corresponding low U/R ratio shows that a high proportion of the requirement is met from within the trees through withdrawal and retranslocation from older tissues. As the retranslocation of a nutrient

Table 23. Contents of N, P, K, Ca and Mg in needle and total litter (kg/ha/an.).

Plots/Components	N	P	K	Ca	Mg
Control					
Needle	25.59	1.83	6.13	11.38	1.79
Others	10.99	0.40	1.49	0.73	0.16
Total	36.58	2.23	7.62	12.11	1.96
Fertilised					
Needle	24.06	1.65	5.43	10.02	1.69
Others	14.66	0.52	1.92	0.71	0.22
Total	38.72	2.17	7.35	10.73	1.91
Saw-dust Treated					
Needle	25.95	1.79	5.91	11.93	1.87
Others	13.55	0.54	2.03	0.97	0.18
Total	39.50	2.33	7.94	12.90	2.05

Table 24. Estimation of retranslocation, requirement and uptake in the needle, branch and bole and the whole tree. Amounts in kg/ha/an

	N	P	K	Ca	Mg
Needle					
a)Total in 1977	148.65	13.30	67.63	21.25	9.74
b)Total in 1978	71.12	6.82	38.19	17.67	4.59
c)Total in litter	25.59	1.83	6.13	11.38	1.79
d)Total leached	0.37	0.27	8.55	6.53	3.07
Retranslocation (T)					
(a-b-c-d)	51.57	4.38	14.76	-14.33	0.29
Requirement(R)	68.43	8.08	46.38	8.02	4.53
Uptake (U)	16.86	3.70	31.62	22.35	4.24
Branch					
a)Total in 1977	92.50	9.64	46.31	30.87	14.49
b)Total in 1978	58.01	5.29	36.77	34.47	7.77
c)Total in dead branch	6.51	0.65	0.65	1.44	0.12
Retranslocation	27.98	3.70	8.89	-5.04	6.60
Requirement	29.30	3.43	13.86	5.73	2.27
Uptake	1.32	-0.27	4.97	10.77	-4.33
Bole					
a)Total in 1977	84.55	13.62	97.59	93.88	21.33
b)Total in 1978	78.92	10.98	94.64	88.87	11.52
c)Total in dead trees	0.69	0.10	0.84	0.73	0.10
Retranslocation	4.94	2.54	2.11	4.28	9.71
Requirement	10.07	1.48	13.89	6.18	0.96
Uptake	5.13	-1.06	11.78	1.90	-8.75
Whole tree					
Total retranslocation	84.49	10.62	25.76	-15.09	16.60
Total requirement	109.28	13.21	74.86	20.20	7.89
Total uptake	24.79	2.59	49.10	35.29	-8.71
U/R	0.227	0.196	0.656	1.747	-

corresponds to its being transferred away from the tissue, a negative retranslocation implies that there is an accumulation of the nutrient in the tissue.

5.5.2. Estimation

An estimate of bark requirement is included to provide a better estimate of total requirement for the bole but no estimate of retranslocation can be obtained for the bark as there is only one value of concentration for each nutrient in the bark. This results in a slight underestimate of retranslocation in the bole. The requirements for the cones are included in the estimate of total tree requirement, and like the bark, there is no estimate of retranslocation as only one value of concentration is available for each nutrient.

5.5.3. Amounts

Large amounts of N, P and K are retranslocated in the trees from the older tissues to the new growth, and the quantities involved can make up to 80% of the total requirement (Table 24). The negative value of retranslocation for Ca indicates that Ca is being accumulated, so that in addition to the requirement for new growth, there is an additional amount equal to that being accumulated. The negative uptake of Mg is probably erroneous as a net overall loss from the trees is not likely to occur in the stand at the present stage of maturity. This anomaly has resulted because the concentrations obtained and used in the first year are much higher than those obtained in the second set of

samples.

In practice between-tree variation appears to have been sufficiently great to mask year to year changes. Negative uptakes were calculated for several components. The implication is that many more sample trees are needed. The expedient adopted here in an attempt, nevertheless, to use these data for the purposes of the investigation, is to apply only one year's nutrient analysis data to the biomass in both years. Turner (1975) also used concentration data from one year with the biomass data from two consecutive years to calculate the amounts retranslocated and taken up through the roots in Douglas fir. With this modification, there is no negative uptake for the total tree budgets, but some components still show negative uptakes (Table 25). The presence of negative uptake for components is, however, not an unlikely phenomenon as inter-component transfers may occur.

Much of the nutrient retranslocation takes place in the needles (which also have the highest requirement for all the different nutrients) while the least retranslocation takes place in the wood (Table 25). The modified nutrient budget shows that retranslocation accounts for a large proportion of the stand requirement for N, P and K, and that uptake of Ca is greater than the requirement for new growth. The budget for Mg shows that a large proportion of the requirement for Mg is met by uptake.

While the U/R ratios for the various nutrients are generally comparable with similar values calculated for Douglas fir and Loblolly pine, they are consistently slightly lower than those

Table 25. Retranslocation, requirement and uptake in needles, branches and boles based on concentration values from 1978 samples.

	N	P	K	Ca	Mg
Needle					
Retranslocation (T)	37.61	5.46	28.77	-10.86	-0.64
Requirement (R)	68.43	8.08	46.38	8.02	4.53
Uptake (U)	30.82	2.62	17.61	18.88	5.17
Branch					
Retranslocation	19.30	2.44	11.17	2.66	1.74
Requirement	29.30	3.43	13.86	5.73	2.27
Uptake	10.00	0.99	2.69	3.07	0.53
Bole					
Retranslocation	4.22	0.70	6.53	-0.62	0.27
Requirement	10.07	1.48	13.89	6.18	0.96
Uptake	5.85	0.78	7.36	6.78	0.69
Total					
Retranslocation	61.13	8.60	46.47	-8.82	1.37
Requirement	109.28	13.21	74.86	20.20	7.89
Uptake	48.15	4.61	28.39	29.02	6.52
U/R	0.441	0.349	0.379	1.437	0.826

estimated for these conifers (Turner, 1975; Switzer and Nelson, 1972). This is because the values of uptake used in these studies are overestimated through the inclusion of the nutrients from aerosols with the estimates for leaching. Apart from these studies there are no other studies in which retranslocation and uptake have been estimated in a similar way and with which comparisons may be made.

5.6. Overall Budget

The various estimates of biomass, nutrient contents and transfers may be combined to construct an overall budget for the above-ground parts of trees at Devilla (Table 26). The total input of nutrients to the forest floor is obtained by adding the amounts in throughfall to the amounts in total litter, while the amount returned by the trees to the forest floor equals the amount in the total litter and the amounts leached from the needles.

Although the soil nutrient content at Devilla was not determined because of difficulties in sampling and analyses (Van den Burg, 1976), an estimate of the contribution of the soil to the overall budget can be made by assuming that the total amount of nutrients released by decomposition of the litter layer equals the amount added through litterfall. As roots and mycorrhizae form an efficient interceptor for leachates and nutrients under the litter layer, most of the nutrients released by decomposition and found in the throughfall would be absorbed and contribute to the total uptake. The difference between total

input to the forest floor and uptake (Table 26, item m)) may be attributed to the soil. A negative value indicates that there is a net removal or loss from the soil while a positive value indicates a gain by the soil.

By relating the various transfers to requirement or uptake, the relative contribution of the various sources of nutrients and processes may be assessed (Turner, 1975; Norton and Young, 1976).

The input by rain and aerosols represent additions to the nutrient capital in the ecosystem and is an important part of the geological cycle of nutrients. The total input of N and P from rain and aerosols is low and makes up less than 2% of the annual requirements of these nutrients (Table 26,n)). The total input of Ca and Mg is higher and accounts for 45 and 27% respectively of their annual requirements. While most of the input of these four elements is from rain, a large proportion of the total input of K is from aerosols in the canopy (Table 26,i)). This high aerosol input of K may be related to the proximity of the study area to agriculture.

Return of nutrients from the trees to the forest floor is an important process in the biogeochemical cycle as the nutrients which are returned are made available for further uptake and recycling. A large proportion of the requirement for Ca and Mg are returned as litter and leachates while approximately one-third of the annual requirement for N and one-fifth of the requirements for P and K are returned in this way (Table 26,o)).

The contribution of the soil to the total requirements for

Table 26. Overall cycling of N,P,K,Ca and Mg in the above-ground parts of trees in Devilla.

Items Amounts (kg/ha/an; except a))	N	P	K	Ca	Mg
a)Total capital in trees	340.0	35.5	217.0	142.5	47.0
b)Requirement	109.3	13.2	74.9	20.2	7.9
c)Retranslocation	61.1	8.6	46.5	-8.8	1.4
d)Uptake	48.2	4.6	28.4	29.0	6.5
e)Litterfall	36.6	2.2	7.6	12.1	2.0
f)Input through rain	1.6	0.4	4.6	8.2	1.6
g)Total in throughfall	2.0	0.5	29.2	15.6	5.2
h)Total leached	0.4	0.3	8.6	6.5	3.1
i)Aerosol input (c-b-d)	0.0	-0.2	16.0	0.9	0.5
j)Total input into system (f+i)	1.6	0.2	20.6	9.1	2.1
k)Total return (e+h)	37.0	2.5	16.2	18.6	5.1
l)Total input into forest floor (e+g or j+k)	38.6	2.7	36.8	27.7	7.2
m)Soil (l-i)	-9.6	-1.9	8.3	-1.3	-0.7
Ratios (%)					
n)Input/Requirement (j/b)	1.5	1.5	27.5	45.0	26.6
o)Return/Requirement (k/b)	33.9	18.9	21.6	92.1	64.6
p)Soil/Requirement (m/b)	8.8	14.4	0.0	6.4	8.8
q)Total leached/Return (h/d)	1.1	12.0	53.1	34.9	60.8

the various nutrients amounts to below 15% (Table 26,p)). No contribution of K from the soil can be estimated for K as the total input of K to the forest floor is greater than the uptake (Table 26, 1), d)).

Other ratios can also be determined from the various transfers in Table 26. The ratio of leaching to the total return (Table 26, q)) shows that more of K and Mg are returned to the soil via rain than via litterfall and this is related to the mobility and solubility of these two ions. The very low ratios for N and P indicates that very small amounts of these two nutrients are lost through leaching and as the negative aerosol contribution suggests, they are withdrawn by the canopy.

CHAPTER 6.

RESULTS AND DISCUSSION IV. EFFECTS OF NITROGEN AVAILABILITY ON PRODUCTION AND NUTRIENT CYCLING

6.1. Introduction

Having determined the degree of internal cycling in trees, it is also important to assess the flexibility of the trees to adapt to different levels of nutrient availability in the soil. In this chapter, the effects of increased and decreased availability of nitrogen on stand characteristics, annual production, nutrient content and litter production will be discussed, followed by the changes in requirement, retranslocation and uptake in response to different levels of nitrogen availability.

6.2. Treatments

While ammonium nitrate was applied to increase the amount of available N in the soil, a short-term deficiency was induced by treating the plots with sawdust and sugar to encourage the development of microorganisms so that less of the soil N is available to the trees. Turner (1975) also applied sawdust and sugar (at higher rates) to create conditions of N shortage in Douglas fir stands. The effects of the treatments may be seen in changes in the number of trees, basal area and annual production of new growth as well as needle litter. The results presented are means of the two replicates (plots) for each of the treatments.

6.3. Stand Characteristics

6.3.1. Mortality

Fewer trees died in the fertilised plots than in control or sawdust treated plots, but the differences are not significant ($P > 0.05$) because the number of samples is low; had more treatment plots and replicates been involved, the differences might have been significant (Table 27).

6.3.2. Growth Increment

The highest increment in mean girth is found in the sawdust treated plots, but as mentioned earlier, increment in mean girth is not a reliable indicator of response to treatment. Basal area increment, however, shows a response that is more in keeping with the treatment applied.

6.4. Annual Production

The highest annual production of biomass in both years is found in the fertilised plot, and the lowest in the sawdust treated plots (Table 27). The differences are however, not significant as the number of replicates and the magnitude of the differences are low. While the higher production in the fertilised plots may be due to the higher total biomass of trees in the plots, the higher percentage change in annual production in the fertilised plots may be due to the treatment.

Table 27 Comparisons of mortality, girth and basal area increments, annual production and needle litter production.

Items	Control Plots	Fertilised Plots	Saw-dust Treated Plots
Mortality (Sum of 2 plots) (no./0.1 ha)	6	2	8
Mean Girth increment (from 1977 - 78) (cm)	1.76	1.08	2.10
Total BA increment (from 1977 - 78) (m/ha)	0.81	1.42	0.84
Annual production (1976 - 77) (t/ha)	17.4	17.6	16.2
Annual production (1977 - 78) (t/ha)	18.1	18.4	16.7
Needle litter production (1977 - 78) (t/ha)	3.5	3.2	3.6
Needle litter production (1978 - 79) (t/ha)	3.4	3.7	3.5
Annual accumulation (1977 - 78) (t/ha)	7.9	8.6	7.0

6.5. Nutrient Content

The levels of N in the needles, first year twigs and the outermost wood ring in the fertilised plots are generally higher than those in the control and the sawdust treated plots (Figures 11 - 13). However, analysis of variance of the data on all the nutrients studied shows that only the levels of N in the first year needles are significantly different with respect to treatments ($P < 0.05$). The absence of any difference in the concentrations of N in the branch and wood and of the other nutrients between fertilised and unfertilised trees has also been reported in other conifers (Heilman and Gessel, 1963a; Salonius, 1977; Safford, Young and Knight, 1977) and may be partly due to the high variance associated with each mean.

6.6. Litter Production

In the first year after treatment, the fertilised plots recorded the lowest needle and total litter production, while the sawdust treated plots had the highest (Figure 14). These values however, are not significantly different from each other ($P > 0.05$). In the second year, the fertilised plots had the highest needle and total litter production, but again, the differences were not significant. The control and sawdust treated plots showed slight decreases in needle litter production but the fertilised plots recorded significant increases in both needle and total litter production.

A similar decrease in needle litter production in the first

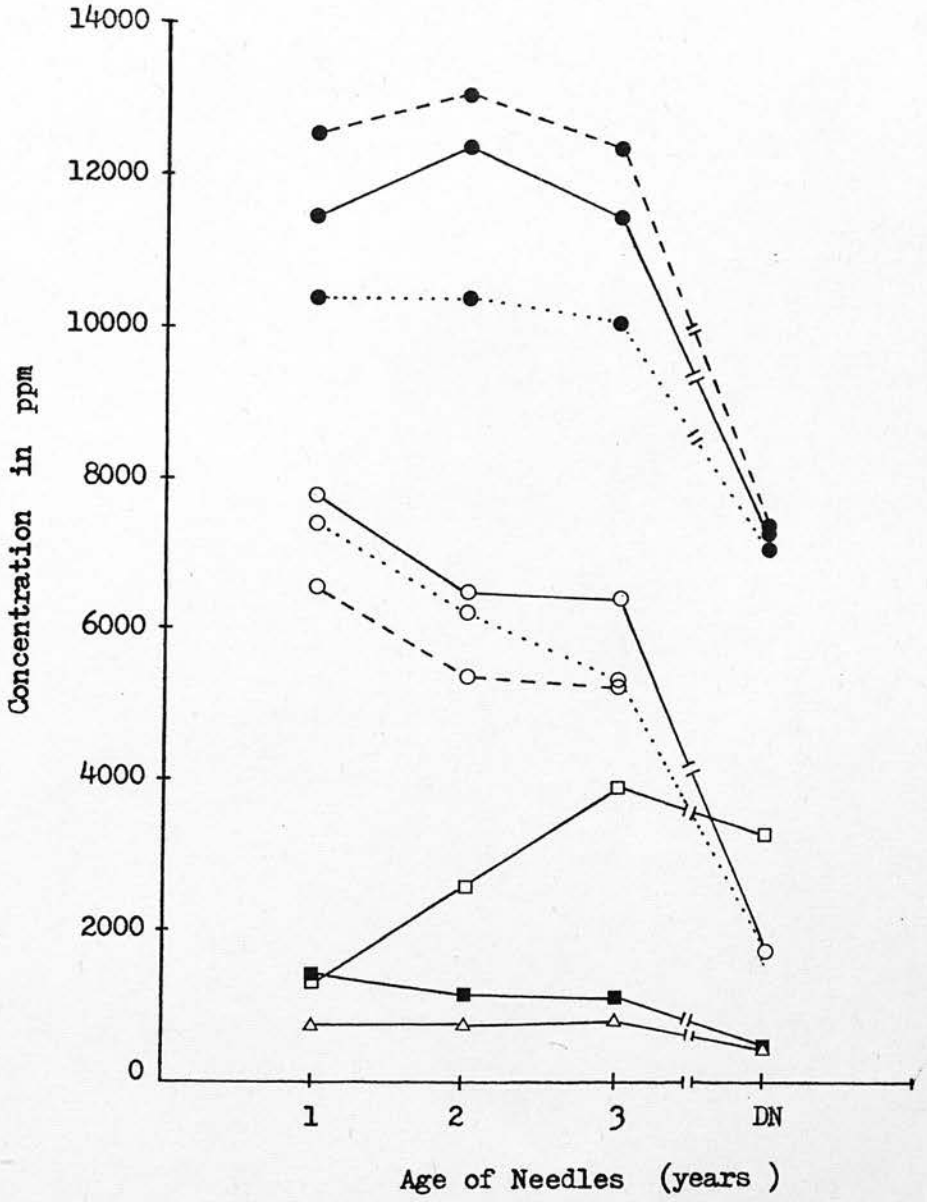

Figure 11. Concentrations of N (●), P (■), K (○), Ca(□) and Mg (△) in first- , second- and third-year and over needles from control (——), fertilised (– – –) and sawdust-treated (·····) plots. Values for fertilised and sawdust-treated trees not included if they are similar to those for the control trees. (DN = Dead Needles)

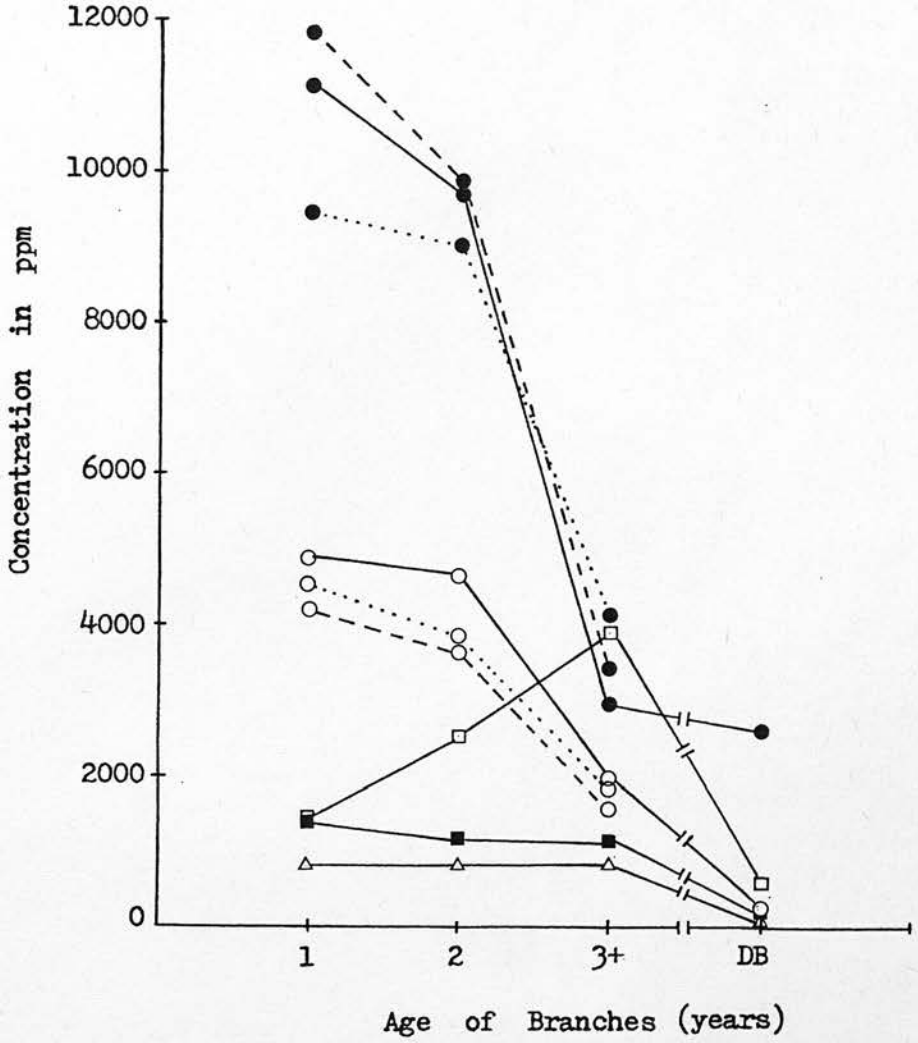

Figure 12. Concentrations of N (●), P (■), K (○), Ca (□) and Mg (△) in first-, second- and third-year and over branches and dead branches (DB) in control (——), fertilised (- - -) and sawdust-treated plots(·····).Values for fertilised and sawdust-treated trees not included if they are similar to those for the control trees.

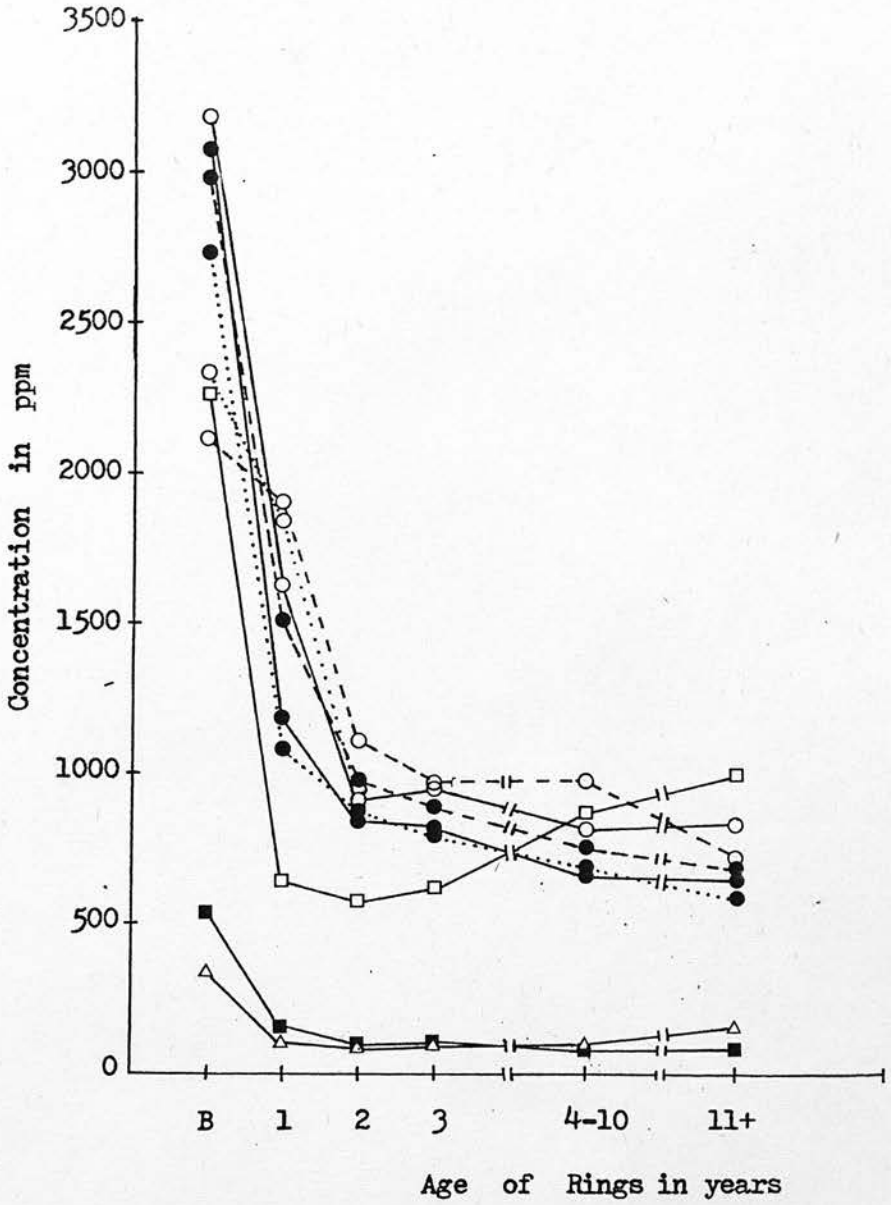

Figure 13. Concentrations of N (●), P (■), K (○), Ca (□) and Mg (△) in the bole bark (B) and wood rings of different ages in control (——), fertilised (– – –) and sawdust-treated (·····) plots. Values for fertilised and sawdust-treated trees are not included if they are similar to those for the control trees.

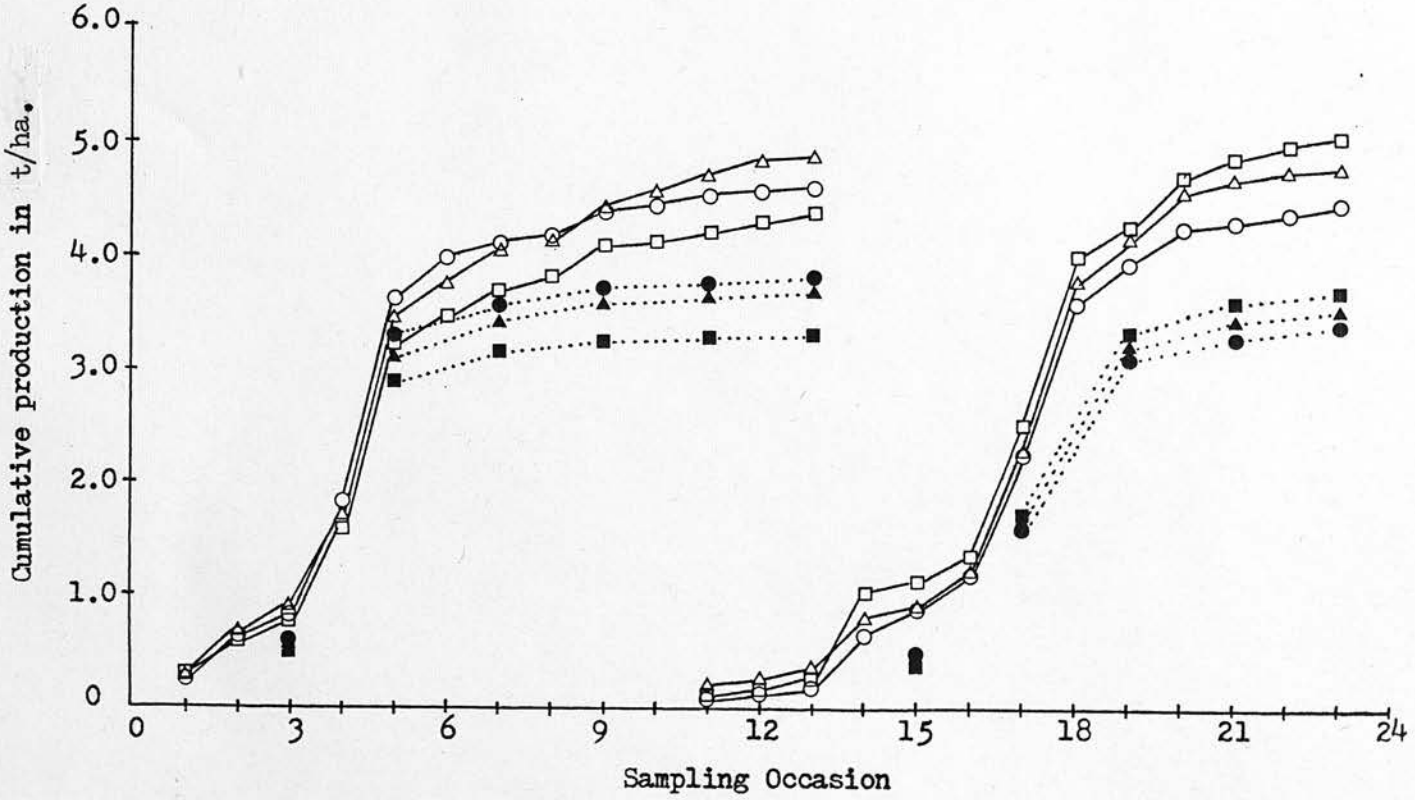

Figure 14. Cumulative production of total (open symbols) and needle (solid symbols) litter in the Control (○, ●), Fertilised (□, ■) and Sawdust treated (△, ▲) plots from 26/5/77 and 30/3/78. Dates corresponding to the different sampling occasions are listed in the Appendix (Table VI).

year following the application of fertilisers followed by an increase in needle litter production in subsequent years has also been found in Corsican and Loblolly pines and is due to the increased retention of older needles in the first year after treatment, followed by the fall of more and perhaps heavier needles in subsequent years (Miller and Miller, 1967; Miller, Cooper and Miller, 1976; Wells, Nicholas and Buol, 1975).

6.7. Translocation and Uptake

The amounts of N in the current year components (that is requirement, as defined earlier; but the use of the term requirement in the present context might be misleading, as requirement implies a demand for a nutrient which may or may not be available) after treatment is related directly to the supply and availability of N in the soil (Table 28). While the absolute amounts retranslocated do not vary much, the amounts of annual uptake increase from 38kg/ha in the N deficient sawdust treated plots to 66kg/ha in the fertilised plots. Uptake as a fraction of requirement also increases while retranslocation decreases with the availability of N. Turner (1975) also found a similar increase in uptake and a corresponding decrease in retranslocation with increasing supply of N in Douglas firs.

While the overall balances of P and Mg did not alter with treatment, the balance of K for both the fertilised and sawdust treated plots showed sharp increases in the amounts retranslocated, resulting in very low uptake to requirement ratios. Although this change might be due to some changes in the internal ionic

Table 28. Comparison of total retranslocation (T), requirement (R) and uptake (U) (kg/ha/an).

	N	P	K	Ca	Mg
Control Plots					
Retranslocation (T)	61.13	8.60	46.47	-8.82	1.37
Requirement (R)	109.28	13.21	74.86	20.20	7.89
Uptake (U)	48.15	4.61	28.39	29.02	6.52
U/R	0.441	0.349	0.379	1.437	0.826
Fertilised Plots					
Retranslocation	55.68	8.72	66.24	11.84	0.49
Requirement	122.10	13.04	68.29	18.73	7.98
Uptake	66.42	4.32	2.05	6.89	7.49
U/R	0.544	0.331	0.030	0.368	0.939
Saw-dust Treated Plots					
Retranslocation	53.64	8.72	61.28	-7.19	0.40
Requirement	92.54	11.76	66.25	18.09	7.39
Uptake	38.90	3.04	4.97	25.28	6.99
U/R	0.420	0.258	0.075	1.397	0.946

balance within the trees resulting from the treatment, it is more likely the result of using the concentrations from the control plots for the estimation of the content in 1977. This might also account for the rather low U/R ratio for Ca in the fertilised plots since the U/R ratio in the sawdust treated plots did not show any change.

CHAPTER 7.

GENERAL DISCUSSION

The production of organic matter in plants is dependent upon the supply and availability of various essential elements. Forest trees may obtain these nutrients from two main sources, namely, the reserves in the soil (including the forest floor) and the nutrient capital within the trees.

In young stands, the nutrient capital within the trees is low in relation to the amounts external to the trees (in the soil and in the understorey vegetation which may be well developed) and much of the requirement for growth is met by uptake from the soil.

As a stand matures, more nutrients become incorporated into the trees as well as in the organic matter on the forest floor, so that in some cases, the supplies in the soil may become limiting. When this occurs, the supplies of nutrients in the forest floor as well as in the tree become the major contributors to requirement (Turner, 1975). While the availability of nutrients already within the trees is influenced by their chemical mobility and solubility, the availability of the nutrients in the forest floor for uptake is determined by the rate of decomposition of the organic matter and the presence and activity of mycorrhizae.

Although decomposition of coniferous litter is slow and the soil at Devilla, being derived from glacial till and sandstone,

is not very fertile, the total amount of nutrients available for uptake does not seem to have limited the production of biomass at Devilla. The low concentrations of N, P and K in the soil and the litter layer may have contributed to the low uptake/requirement ratios for these elements. The corresponding high retranslocation/requirement ratios show that a large proportion of the requirement for each of these elements is met by internal cycling. This ability to retranslocate N, P and K within the trees to meet growth requirements has also been reported in Loblolly pine and Douglas fir (Switzer and Nelson, 1972; Turner, 1975) and may be a more common phenomenon in trees than would seem to be indicated by the paucity of studies on this aspect of the nutrient cycle.

When the supply of N in the soil is decreased, its uptake is lowered and retranslocation is increased to make up the total requirement. With increased redistribution, more nutrients are withdrawn from the older tissues, resulting in the early senescence of tissues and a higher production of needles and total litter.

When the supply of N in the soil is increased, uptake is increased and retranslocation is reduced. The corresponding decrease in withdrawal of nutrients from the older tissues results in increased retention of needles and a lower needle litter production in the first year after treatment. The fall of these needles and of more and heavier needles produced as a result of treatment leads to increased needle litter production

in subsequent years.

While this experiment on the response of the nutrient cycle to nutrient availability was restricted to nitrogen, it is possible that the cycles involving P, K and even Mg could respond in a similar way, ie. retranslocation of the element would increase with a decreased uptake resulting from a decreased availability in the soil and retranslocation would decrease with an increase in uptake resulting from an increased supply. Calcium, however, would be expected to behave differently, since its chemical immobility results in low or even negative retranslocation.

This ability of trees to alter their dependence on internal and external sources of nutrients enables them to tolerate temporary shortages and grow on sites of low fertility as well as to maintain improved growth for a number of years subsequent to fertiliser application (Miller and Miller, 1976).

The quantification of the various components and transfers in the nutrient cycle requires the accurate determination of biomass, nutrient content as well as transfers such as litterfall and input from rain.

For estimating the biomass of trees, it was found that the regression method used was sufficiently accurate and reliable, especially when the estimates were calculated on an area basis. Although the use of a multiple of girth and height as the x-variable in these regressions is preferable (Madgwick, 1971), the slight increase in accuracy was not considered worthwhile in the present study since a very good fit was already obtained

with log(girth) as the independent variable. Further, the heights obtained in different years are inconsistent because of differences in instruments as well as in their use, ie. values obtained differed when measurements were taken from different compass directions.

The bias which arose from taking the anti-logs to give the estimated biomass in arithmetic values was very low because the regressions were highly significant ($P < 0.01$). Since the amount of correction required to compensate for this bias was less than the coefficient of variation of the sampled mean, it was not applied.

The regression coefficient, b, tends to increase with age (Cousens, pers. comm.) as the form of the tree changes. However the regressions obtained in the first year were used to estimate the biomass in the second year because the regression coefficients calculated from the biomass data (Appendix Table III) of all the trees collected in 1978 were not significantly different from those based on the first set of samples ($P > 0.05$).

The method used for estimating retranslocation in the present study is reasonable as most possible transfers have been considered. Increased accuracy in the estimates of the other transfers as well as the nutrient contents involved should result in better estimates of retranslocation and hence of uptake.

The coefficients of variation of the mean concentrations of most of the nutrients in the various components are generally below 10%, exceptions being the bark and the branches, where

coefficients of variation of up to 30% are recorded (Appendix Table IV). While the precision of the estimates may be increased by taking more samples, it may also be achieved by further subdividing some of these components; for example, older branches may be subdivided into various sections based on girth (Brown, 1976; Young and Carpenter, 1976).

Although most of the nutrient concentrations obtained in the second year were not significantly different from those obtained in the first year, the differences between the mean values in some components are quite high. These differences could be due to differences in the time of collection, position in the tree and natural variation between trees. Non-destructive sampling may be used to minimise variations arising from some of these differences. Samples of the various components may be collected from specific parts of a number of specified trees within the various plots. Further, concentrations of the various nutrients in the different components should be determined at regular intervals so that overall trends may be determined and minor fluctuations compensated for.

Although the method of estimating the amounts of nutrients leached from the amounts in rainfall and throughfall using regressions (Miller, Cooper and Miller, 1976) is relatively new, the results obtained are consistent with the known chemical properties and responses of the various nutrients to leaching . However, as the parameters of the regression have not been defined in relation to the physiological and chemical nature of leaching, more

studies are required.

Production of needles, cones and fine twig litter may be estimated directly and fairly accurately using litter traps. However, the accumulation of dead branches is more difficult to assess as their fall is not even and many remain attached to trees. The annual accumulation of dead trees is also difficult to assess as many dead trees remain upright. The production of dead branches was therefore indirectly estimated as the difference in the biomass of live branches from one year to the next, while that of dead trees was assumed equivalent to the biomass of the same trees when they were alive.

While the application of nitrogen fertilisers to tree crops is a common technique for improving production as well as for studying its effects on the nutrient cycle (Armson, 1976), the application of sawdust - sugar to intensify nutrient deficiency is less common and was first used in a stand of trees by Turner (1975). Although some of the changes such as changes in concentration of nitrogen in the various tissues, are evident after only one year, many growth responses are only evident in the second year after treatment (Mayhead, 1976). The short duration of this study, however, prevents the continued measurement of girth and concentration values beyond the second year when the results of such treatments could become more conclusive. The studies of response may also be improved by increasing the number of treatments to include higher levels of N availability, such as 200 and/or 400 kg/ha of N so that luxury uptake may be demonstrated, as well as more intense levels of nitrogen deficiency

in the soil.

Tree roots and ground vegetation have not been considered in this study even though roots may account for up to 20% of the total biomass of trees (Ovington, 1957a). Roots were excluded from the study because of the practical difficulties involved in their excavation, while the ground vegetation was excluded because large areas in the plots were not covered by any such vegetation and large numbers of samples would have been required to provide reliable estimates of the biomass of this component.

Studies on nutrient cycling in ecosystems should ideally extend over a number of years so that chance fluctuations are not interpreted as mean values. Further, the response of tree crops to different treatments may only become evident after a number of years.

In the limited time available for this study, the uptake and internal cycling of nutrients in the above-ground parts of the trees in Devilla have been investigated. While some information on the nutrient capital in the above-ground parts of trees and patterns of cycling has been obtained, the total nutrient budget for the whole forest ecosystem is still incomplete. Determination of biomass production and losses and nutrient contents of the roots of the trees and the understorey vegetation, as well as the nutrient content of the litter layer and the soil would enable the total nutrient budget of the ecosystem to be constructed.

Apart from these studies to complete the nutrient budget

for Devilla, similar studies involving Scots pine stands of different ages could be conducted to relate the degree of internal cycling to the age and development of the stands. These studies could also be extended to other species to examine whether retranslocation is a general phenomenon in trees.

SUMMARY

1) Six study plots were established at Devilla Forest and the girths and heights of all the trees in the plots were measured.

2) A sample of ten trees was harvested and regressions relating the weights of the various components to girths were calculated.

3) The biomass of the above-ground parts of all the trees in the plots was estimated by applying the regressions on the girth data obtained from the enumeration of the plots.

4) The nutrient concentrations and contents of the different components of the tree were determined.

5) Rainfall and throughfall and their nutrient contents were determined and the amounts leached from the canopy estimated.

6) Total and needle litter production and their contents of N, P, K, Ca and Mg were determined.

7) Retranslocation was estimated by accounting for all possible losses and/or transfers from the tissues after one year.

8) Uptake was estimated from the annual requirement and retranslocation.

9) The effects of different levels of nitrogen availability in the soil on retranslocation and uptake were studied by applying a nitrogen fertiliser in one treatment and sawdust and sugar in another.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Mr. J. E. Cousens, for his guidance and help. His interest and advice has been most encouraging and my association with him has been most rewarding.

My thanks also go to Professor C.J. Taylor and Dr. D.C. Malcolm for their help and advice during the course of this study and the write-up of this thesis; to Derek Scott for his assistance in the field and in the collection of some samples and others in this Department who have helped in one way or another.

I would also like to thank the Association of Commonwealth Universities for their award of a Commonwealth Scholarship during the last three years and the Forestry Commission for permission to work in Devilla Forest, as well as Universiti Pertanian Malaysia (Agriculture University of Malaysia) for leave to undertake this study.

Last but not least, I would like to thank my family for their support and encouragement. I am most grateful to my wife, Irene, who has been most helpful and encouraging and yet most tolerant of my shortcomings in the last few months. To her, and to our Christopher and Jonathan, I dedicate this thesis.

REFERENCES

Alestalo, A. (1973). On the possibilities of the utilisation of needles and bark. In: (young, H.E., ed.) IUFRO Biomass Studies, pp. 429 - 442. University of Maine, Orono.

Allen, S.E., Grimshaw, H.M., Parkinson, J.A. and Quarmby, C. (1974). Chemical analysis of ecological materials. Blackwell Scientific Publications, Oxford. 565 pp.

Anderson, M.L. and Fairbairn, W.A. (1955). Division of Scotland into climatic sub-regions as an aid to silviculture. Bull. For. Dept. Univ. Edinb. No. 1.

Armson, K.A. (1976). Fertiliser studies as a basic technique. In: XVI IUFRO World Congress Proceed. Div.I. Norway, pp. 142 - 147.

Attiwill, P.M. and Ovington, J.D. (1968). Determination of forest biomass. Forest Sci. 14: 13 - 15.

Baker, J.B., Switzer, G.L. and Nelson, L.E. (1974). Biomass production and nitrogen recovery after fertilisation of young Loblolly pines. Soil Sci. Soc. Amer. Proc. 38: 958 - 961.

Barker, P.R. (1966). Studies of dry matter production and mineral uptake in Pinus sylvestris L., in relation to certain soil properties. B.Sc. Hons. Thesis, Edinburgh University.

Baskerville, G.L. (1965). Estimation of dry weight of tree components and total standing crop in conifer stands. Ecology, 46: 867 - 869.

Baskerville, G.L. (1966). Dry matter production in immature Balsam Fir stands : roots, lesser vegetation and total stand. Forest Sci. 12: 49 - 53.

Baskerville, G.L. (1972). Use of logarithmic regressions in the estimation of plant biomass. Can. J. For. Res., 2: 49 - 53.

Beauchamp, J.J. and Olson, J.S. (1973). Corrections for bias in regression estimates after logarithmic transformations. Ecology, 54: 1403 - 1407

Bray, J.R. and Gorham, E. (1964). Litter production in forests of the world. Adv. Ecol. Res., 2: 101 - 157.

Brown, J.K. (1976). Predicting crown weights for eleven Rocky Mountain conifers. In: (Young, H.E., ed.) Oslo Biomass Studies, pp. 103 - 116. University of Maine, Orono.

Carlisle, A., Brown, A.H.F. and White, E.J. (1967). The nutrient content of rainfall and its role in the forest nutrient cycle. In: XIV IUFRO Congress Munich 1967 Vol. II: 145 - 158.

Carlisle, A. and Brown, A.H.F. (1968). Biological flora of the British Isles: Pinus sylvestris L. J. Ecol.,56: 269 - 307.

Crooke, W.M. and Simpson, W.E. (1971). Determination of ammonium in Kjeldahl digests of crops by an automated procedure. J. Sci. Fd. Agric., 22: 9 - 10.

Crow, T.R. (1971). Estimation of biomass in an even aged stand - - regression and mean tree techniques. In: (Young, H.E., ed.) Forest Biomass Studies, pp. 35 - 50. University of Maine, Orono.

Curlin, J.W. (1970). Nutrient cycling as a factor in site productivity and forest fertilisation. In: (Youngberg, C.T. and Davey , C.B., eds.) Tree growth and forest soils, pp. 313 - 325. Oregon State University Press, Corvallis.

Dice, S.F. (1970). The biomass and nutrient flux in a second growth Douglas fir ecosystem (a study in quantitative ecology). Unpublished Ph.D. thesis, University of Washington, Seattle.

Epstein, E. (1971). Mineral nutrition of plants: Principles and perspectives. John Wiley and Sons, New York. 412 pp.

Ericsson, A. (1978). Seasonal changes in translocation of ^{14}C from different age-classes of needles on 20-year-old Scots pine trees (P. sylvestris). Physiol. Plant. 43: 351 - 358.

Feller, M.C. (1977). Nutrient movement through western Hemlock-western red cedar ecosystems in southwestern British Columbia. Ecology, 58: 1269 - 1283.

Forrest, W.G. and Ovington, J.D. (1970). Organic matter changes in an age series of Pinus radiata plantations. J. Appl. Ecol. 7: 177 - 186.

Foster, N.W. and Morrison, I.K. (1976). Distribution and cycling of nutrients in a natural Pinus banksiana ecosystem. Ecology, 57: 110 - 120.

Gash, J.H.C. and Stewart, J.B. (1977). The evaporation from Thetford Forest during 1975. J. Hydrol. 35: 385- 96.

Hakkila, P. (1971). Branches, stumps and roots as a future raw material source in Finland. In: (Young, H.E., ed.) Forest Biomass Studies, pp. 51 - 64. University of Maine, Orono.

Hakkila, P. (1973). Towards the utilisation of stump and root wood. In: (Young, H.E., ed.) IUFRO Biomass Studies, pp. 451 - 466. University of Maine, Orono.

Hamilton, G.J. and Christie, J.M. (1971). Forest Management Tables (Metric). Forestry Commission Booklet No. 34. HMSO London. 201 pp.

Heilman, P.E. and Gessel, S.P. (1963a). The effect of nitrogen fertilisation on the concentration and weight of nitrogen, phosphorus and potassium in Douglas fir trees. Soil Sci. Soc. Amer. Proc. 27: 102 - 105.

Heilman, P.E. and Gessel, S.P. (1963b). Nitrogen requirements and the biological cycling of nitrogen in Douglas fir stands in relationship to the effects of nitrogen fertilisation. Plant Soil, 18: 386 - 402.

Henderson, G.S. and Todd, D.E. (1972). Nutrient return in throughfall for four forest stand types and its importance in annual nutrient cycles. Eastern Deciduous Forest Biome Rep. No. 72 - 154.

Henderson, G.S. and Harris, W.F. (1973). An ecosystem approach to characterisation of the nitrogen cycle in a deciduous forest watershed. In: (Bernier, B. and Winget, C.H., ed.) Forest Soils and Forest Land Management, Quebec, pp. 179 - 193.

Henderson, G.S., Harris, W.F., Todd, Jr.D.E. and Grizzard, T. (1977). Quantity and chemistry of throughfall as influenced by forest type and season. J. Ecol. 65: 365 - 374.

Keays, J.L. (1971). Complete tree utilisation. Resumé of a literature review. In: (Young, H.E., ed.) Forest Biomass Studies, pp. 93 - 104. University of Maine, Orono.

Kimmins, J.P. (1973). Some statistical aspects of sampling throughfall precipitation in nutrient cycling studies in British Columbian coastal forest. Ecology, 54: 1008 - 1019.

Kimmins, J.P. and Krumlik, G.J. (1976). On the question of nutrient losses accompanying whole tree logging. In: (Young, H.E., ed.) Oslo Biomass Studies, pp. 41 - 54. University of Maine, Orono.

Krumlik, G.J. and Kimmins, J.P. (1973). Studies of biomass distribution and tree form in old virgin forests in the mountains of south coastal British Columbia, Canada. In: (Young, H.E.,ed.) IUFRO Biomass Studies, pp. 361 - 374. University of Maine, Orono.

Leaf, A.L. and Leonard, R.E. (1976). Use of fertilisers for non-wood production benefits. In: XVI IUFRO World Congress Proceed. Div.I. Norway, pp. 114 - 127.

Lehtonen, I. (1977). Ravinteiden kierto eraasa mannikossa. III. Maaperan, kasvillisuuden ja sadeveden ravinnepitoisuuksien vaihtelu. Silva Fenn., 11: 184 - 194.

Lehtonen, I. (1978). Ravinteiden kierto eraasa mannikossa. IV. Fytomassan ja Ravinteiden maara. Silva Fenn., 12: 47 - 55

Maclean, D.A. and Wein, R.W. (1977). Nutrient accumulation for postfire jack pine and hardwood succession patterns in New Brunswick. Can. J. For. Res., 7: 562 - 578.

Madgwick, H.A.I. (1964). The chemical composition of foliage as an index of nutritional status in red pine (Pinus resinosa Ait.) Plant and Soil, 21: 70 - 80.

Madgwick, H.A.I. (1971). The accuracy and precision of estimates of dry matter in stems, branches and foliage in an old field Pinus virginiana stand. In: (Young, H.E., ed.) Forest Biomass Studies, pp. 105 - 114. University of Maine, Orono.

Madgwick, H.A.I. (1976). Mensuration of forest biomass. In: (Young, H.E., ed.) Oslo Biomass Studies, pp. 11 - 27. University of Maine, Orono.

Madgwick, H.A.I. and Ovington, J.D. (1959). The chemical composition of precipitation in adjacent forest and open plots. Forestry, 32: 14 - 22.

Madgwick, H.A.I. and Satoo, T. (1975). On estimating the above ground weights of tree stands. Ecology, 56: 1446 - 1450.

Malkonen, E. (1973). Effect of complete tree utilisation on the nutrient reserves of forest soils. In: (Young, H.E., ed.) IUFRO Biomass Studies, pp. 375 - 386. University of Maine, Orono.

Malkonen, E. (1974). Annual primary production and nutrient cycle in some Scots pine stands. Comm. Inst. For. Fenn. 84.5 : 87 pp.

Malkonen, E. (1976). Effect of whole tree harvesting on soil fertility. Silva Fenn., 10: 157 - 164.

Mayhead, G.J. (1976). Forest fertilising in Great Britain. Fertiliser Soc. of London Proceeds (158). 18 pp.

Miller, H.G. and Miller, J.D. (1967). Changes in weight and nutrient content of litterfall beneath Corsican pine following application of nitrogen. XIV. IUFRO Congress, Munich 1967 : 335 - 351.

Miller, H.G., Cooper, J.M. and Miller, J.D. (1976). Effects of nitrogen supply on nutrients in litterfall and crown leaching in a stand of Corsican pine. J. Appl.Ecol., 13: 233 - 248.

Miller, H.G. and Miller, J.D. (1976). Effect of nitrogen supply on net primary production in Corsican pine. J. Appl. Ecol., 13: 249 - 256.

Miller, H.G., Miller, J.D. and Pauline, O.J.L. (1976). Effect of nitrogen supply on nutrient uptake in Corsican pine. J. Appl. Ecol.,13: 955 - 966.

Miller, W.F. (1966). Annual changes in foliar nitrogen, phosphorus and potassium levels of Loblolly pine (Pinus taeda) with site and weather factors. Plant and Soil, 24: 369 - 378.

Morrison, I.K. (1974). Within tree variation in mineral content of leaves of young Balsam fir. For. Sci. 20: 276 - 278.

Mountford, M.D. and Bunce, R.G.H. (1973). Regression sampling with allometrically related variables with particular reference to production studies. Forestry, 46: 203 - 212.

Norton, S.A. and Young, H.E. (1976). Forest biomass utilisation and nutrient budgets. In: (Young, H.E., ed.) Oslo Biomass Studies, pp. 55 - 74. University of Maine, Orono.

Ogawa, H., Yoda, K. and Kira, T. (1961). A preliminary survey on the vegetation of Thailand. Nature and Life in S.E. Asia, 1: 21 - 57.

Olson, J.S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. Ecology,44: 322 - 331.

Olszowski, J. (1976a). The effect of fertilisation on a pine forest ecosystem in an industrial region. I. Forest

stand volume increment. Ekol. Pol., 24(3): 285 - 297.

Olszowski, J. (1976b). The effect of fertilisation on a pine forest ecosystem in an industrial region. VII. Summary of the studies. Ekol. Pol., 24(3): 359 - 363.

Olszowski, J. and Warteriesiewicz, M. (1976). The effect of fertilisation on a pine forest ecosystem in an industrial region. II. Sulphur content and some morphological characters of the needles. Ekol. Pol., 24(3): 299 - 306.

Ovington, J.D. (1957a). The volatile matter, organic carbon and nitrogen contents of tree species grown in close stands. New Phytol., 56: 1 - 11.

Ovington, J.D. (1957b). Dry matter production by Pinus sylvestris. Ann. Bot. Lond.N.S., 21: 287 - 314.

Ovington, J.D. (1959a). Mineral content of plantations of Pinus sylvestris L. Ann. Bot. Lond. N.S., 23 : 75 - 88.

Ovington, J.D. (1959b). The circulation of minerals in plantations of Pinus sylvestris L. Ann. Bot. Lond. N.S., 23: 230 - 239.

Ovington, J.D. (1959c). The calcium and magnesium contents of tree species grown in close stands. New Phytol., 58: 164 - 175.

Ovington, J.D. (1960). The nutrient cycle and its modification through silviculture practices. Proc. Fifth World Forest Congress, 1: 533 - 538.

Ovington, J.D. (1962). Quantitative ecology and the woodland ecosystem concept. Adv. Ecol. Res., 1: 103 - 192.

Ovington, J.D. (1968). Some factors affecting nutrient distribution within ecosystems. In: (Eckardt, F.E., ed.) Functioning of terrestrial ecosystems at the primary production level. Proceedings of the Copenhagen Symposium. Paris, UNESCO., pp. 95 - 105.

Ovington, J.D. and Madgwick, H.A. (1959). Distribution of organic matter and plant nutrients in a plantation of Scots pine. For. Sci., 5: 344 - 355.

Ovington, J.D., Forrest, W.G. and Armstrong, J.S. (1968). Tree biomass estimation. In: (Young, H.E., ed.) Symp. on Primary Productivity and Mineral cycling in Natural Ecosystems, pp. 4 - 31. University of Maine, Orono.

Rennie, P.J. (1956). The uptake of nutrients by mature forest growth. Plant and Soil, 7: 49 - 95.

Rennie, P.J. (1966). A forest sampling procedure for nutrient uptake studies. Comm. For. Rev., 45: 119 - 127.

Ribe, J.H. (1973). A study of multi-stage and dimensional analysis sampling of Puckerbrush stands. In: (Young, H.E.,ed.) IUFRO Biomass Studies, pp. 119 - 130. University of Maine, Orono.

Rochow, J.J. (1974). Estimates of above-ground biomass and primary productivity in a Missouri forest. J. Ecol., 62: 567 - 577.

Rolfe, G.L., Akhtar, M.A. and Arnold, L.E. (1977). Nutrient distribution and flux in a mature oak-hickory forest. For. Sci., 24: 122 - 130.

Safford, L.D., Young, H.E. and Knight, T.W. (1977). Effect of soil and urea fertilisation on foliar nutrients and basal area growth of red spruce. Life Sciences and Agr. Expt. St. Bulletin 740. University of Maine, Orono. 27 pp.

Salonius, P.O. (1977). Nutrient concentration in Black Spruce foliage immediately following fertilisation. Soil Sci. Soc. Amer. J., 41: 136 - 139.

Satchell, J.E., Lindley, D.K. and Hibberd, J.K. (1971). Computation of confidence limits for estimates of net primary production. In: (Rosswall,T., ed.) Systems Analysis in Northern Coniferous Forests. Swed. Nat. Sci.Res. Counc. Bull. 14, pp. 75 - 83.

Smith, W.H., Nelson, L.E. and Switzer, G.L. (1963). The characterisation of dry matter and nitrogen accumulation by Loblolly pine (Pinus taeda L.) on poor sites. Soil Sci. Soc. Amer. Proc., 27: 465 - 468.

Snedecor, G.W. (1956). Statistical methods applied to experiments in agriculture and biology. Iowa State University Press. Iowa. 534 pp.

Sokal, R.R. and Rohlf, F.J. (1971). Biometry. W.H. Freeman and Co. San Francisco. 776 pp.

Swank, W.T. and Henderson, G.S. (1976). Atmospheric input of some cations and anions to forest ecosystems in North Carolina and Tennessee. Water Resources Res., 12(3): 541 - 546.

Switzer, G.L., Nelson, L.E. and Smith, W.H. (1966). The characterisation of dry matter and nitrogen accumulation by Loblolly pine (P. taeda). Soil Sci. Soc. Amer. Proc., 30: 114 - 119.

Switzer, G.L. and Nelson, L.E. (1972). Nutrient accumulation and cycling in Loblolly pine (P. taeda L.) plantation ecosystems. The first twenty years. Soil Sci. Soc. Amer. Proc.,36: 143 - 147.

Tarrant, R.F. and Silen, R.R. (1966). Growth and nutrient uptake of irrigated young Ponderosa pine after fertiliser treatments. Soil Sci. Soc. Amer. Proc., 30: 796 - 799.

Turner, J. (1975). Nutrient cycling in a Douglas fir ecosystem with respect to age and nutrient status. Ph. D. thesis, University of Washington, Seattle. 191 pp.

Turner, J. (1977). Effect of nitrogen availability on nitrogen cycling in a Douglas fir stand. For. Sci., 23: 307 - 316.

Turner, J. and Singer, M.J. (1976). Nutrient distribution and cycling in a sub-alpine coniferous forest ecosystem. J. Appl. Ecol., 13: 295 - 301.

Ulrich, B. (1976). Fate of applied nutrients in forest ecosystems. In: XVI IUFRO World Congress Proceed. Div. I. Norway, pp. 106 - 113.

Van den Burg, J. (1976). Problems related to analysis of forest soil fertility. In: XVI IUFRO World Congress Proceed. Div. I. Norway, pp. 148 - 163.

Weaver, G.T. (1976). A comparison of models for estimating production of oak and hickory branches. In: (Young, H.E., ed.) Oslo Biomass Studies, pp. 231 - 250. University of Maine, Orono.

Webber, B.D. (1977). Biomass and nutrient distribution patterns in a young Pseudotsuga menziesii ecosystem. Can. J. For. Res.,7: 326 - 334.

Wells, C.G. and Metz, L.J. (1963). Variation of nutrient content of Loblolly pine needles with season, age, soil and position in crown. Soil Sci. Soc. Amer. Proc., 27: 90 - 93.

Wells, C.G., Nicholas, A.K. and Buol, S.W. (1975). Some effects of fertilisation on mineral cycling in Loblolly pine. In: (Howell, F.G., Gentry, J.B. and Smith, M.H., eds.) Mineral cycling in southeastern ecosystems. Technical Information Center, Oak Ridge, Tennessee, pp. 754 - 764.

White, D.P. (1954). Variations in the nitrogen, phosphorus and potassium contents of pine needles with season, crown position and sample treatment. Soil. Sci. Soc. Amer. Proc., 18: 326 - 330.

White, E.J. and Turner, F. (1970). A method of estimating income of nutrients in a catch of airborne particles by a woodland canopy. J. Appl. Ecol., 7: 441 - 461.

Whittaker, R.H. (1965). Branch dimensions and estimation of branch production. Ecology, 46: 365 - 370.

Whittaker, R.H. and Woodwell, G.M. (1968). Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. J. Ecol., 56: 1 - 25.

Will, G.M. (1959). Nutrient return in litter and rainfall under some exotic conifer stands in New Zealand. N.Z. J. Agric. Res., 2: 719 - 734.

Wright, T.W. and Will, G.M. (1958). The nutrient content of Scots and Corsican pines growing on sand dunes. Forestry, 31 : 13 - 25.

Young, H.E. (1964). The complete tree concept - a challenge and an opportunity . Soc. of Amer. Foresters Proceed. (Denver), pp. 231 - 233.

Young, H.E. (1967). Challenge of complete tree utilisation. For. Products Journ., 18(4): 83 - 86.

Young, H.E. (1975). Utilisation of forest residues - a segment of the complete tree concept. Soc. Amer. Foresters Proceed. (Washington, D.C.), 6 pp.

Young, H.E. and Guinn, V.P. (1966). Chemical elements in complete mature trees of seven species in Maine. Tappi., 49(5): 190 - 197.

Young, H.E. and Carpenter, P.N. (1976). Sampling variation of nutrient element content within and between trees of the same species. In: (Young, H.E., ed.) Oslo Biomass Studies, pp. 75 - 100. University of Maine, Orono.

Zinke, P.J. (1966). Forest interception studies in the United States. Int. Symp. For. Hydrol., pp. 137 - 160. Pergamon Press, Oxford.

APPENDICES

Table I. Girth data of trees in 1976,1977 and 1978 (cm)

a) Control Plot C 1

TREE NO.	GIRTH76	GIRTH77	GIRTH78
1101	49.9	51.0	51.0
1102	54.0	54.6	56.0
1103	62.4	63.3	0.5 *
1104	24.2	24.2	24.2
1105	51.4	51.9	52.6
1106	50.7	50.8	51.5
1107	22.0	0.0	0.0 @
1108	73.5	74.8	75.9
1109	43.0	43.4	50.2
1110	34.5	35.2	0.5
1111	26.6	26.6	26.6
1112	31.4	31.5	31.6
1113	41.2	42.2	42.5
1114	58.0	58.3	59.0
1115	29.2	29.2	0.0
1116	39.5	40.2	40.9
1117	20.1	0.0	0.0
1118	55.6	56.8	58.3
1119	47.6	48.1	48.9
1120	42.9	43.8	44.4
1121	53.3	54.5	55.6
1122	75.6	76.2	76.8
1123	75.3	77.5	79.5
1124	26.2	26.2	26.2
1125	50.6	51.0	51.8
1126	33.3	33.3	33.5
1127	42.3	42.9	43.3
1128	29.2	29.5	29.5
1129	21.2	20.8	20.8
1130	55.3	60.5	61.0
1131	39.6	40.1	40.6
1132	37.0	37.4	37.9
1133	35.2	35.2	35.2
1134	54.6	56.1	57.1
1135	53.1	53.5	54.6
1136	59.1	59.7	60.4
1137	56.8	57.3	58.2
1138	24.0	24.5	24.5
1139	28.9	29.2	29.9
1140	40.2	41.0	42.0
1141	27.3	27.3	27.3
1142	58.1	59.6	60.5
1143	38.5	39.4	40.4
1144	66.6	67.4	69.2
1145	62.8	63.7	64.9

* 0.5 indicates that tree was sampled in 1978
@ 0.0 indicates that tree has died since the last measurement

Table I a). continued,

TREE NO.	GIRTH76	GIRTH77	GIRTH78
1146	55.2	57.3	59.4
1147	40.8	40.9	40.9
1148	32.2	32.3	32.3
1149	33.9	34.0	34.1
1150	40.0	40.3	40.8
1151	71.6	72.8	74.6
1152	58.9	60.5	62.0
1153	51.3	51.4	51.5
1154	43.9	44.6	45.7
1155	45.3	45.5	45.7
1156	29.2	29.2	29.2
1157	57.1	57.8	59.0
1158	22.4	0.0	0.0
1159	35.2	35.3	35.5
1160	47.0	47.3	47.6
1161	52.7	52.9	53.8
1162	36.6	37.2	38.1
1163	37.6	37.8	38.2
1164	55.3	56.3	57.8
1165	31.6	31.8	32.1
1166	64.8	66.2	67.1
1167	52.3	52.3	53.1
1168	65.8	67.2	68.6
1169	48.5	49.3	51.1
1170	54.2	54.8	56.0
1171	28.3	28.4	28.7
1172	19.4	19.4	19.4
1173	34.2	34.4	34.4

b) Control Plot C 2

TREE NO.	GIRTH76	GIRTH77	GIRTH78
1201	50.0	51.2	52.4
1202	73.6	74.9	76.1
1203	83.2	84.8	86.8
1204	33.3	33.3	33.4
1205	59.1	60.0	60.1
1206	56.4	56.9	57.6
1207	63.2	64.0	0.5
1208	71.4	72.6	74.1
1209	30.4	30.3	30.3
1210	53.9	54.6	55.8
1211	30.9	30.8	30.8
1212	38.2	38.3	38.5
1213	50.0	51.2	52.7
1214	39.0	39.2	39.6
1215	27.6	27.6	27.6
1216	23.5	23.7	24.0
1217	32.2	32.2	32.2
1218	87.1	88.8	90.6
1219	37.9	38.6	39.3
1220	25.5	25.5	25.5
1221	53.1	53.5	53.9
1222	40.3	41.0	41.7
1223	21.4	21.4	0.5
1224	22.9	22.9	22.9
1225	75.8	78.9	79.7
1226	75.4	76.8	78.3
1227	60.0	61.7	63.0
1228	61.7	62.6	63.5
1229	51.0	52.0	53.2
1230	48.4	48.9	49.4
1231	82.6	84.0	86.0
1232	57.1	58.0	59.0
1233	60.5	61.3	62.2
1234	64.2	66.2	68.1
1235	33.9	33.9	33.9
1236	77.7	79.3	81.3
1237	46.3	46.3	46.6
1238	55.4	56.8	58.3
1239	64.9	65.6	67.1
1240	66.8	68.4	69.9
1241	30.9	30.9	31.1
1242	79.3	80.6	82.1
1243	73.0	74.2	75.4
1244	44.3	44.7	45.1
1245	39.8	40.0	41.5

Table I b). continued,

TREE NO.	GIRTH76	GIRTH77	GIRTH78
1246	19.2	0.0	0.0
1247	60.7	61.6	63.0
1248	73.4	75.3	77.6
1249	54.9	55.3	55.9
1250	58.6	59.5	60.8
1251	64.9	66.1	67.8
1252	40.2	40.5	41.2
1253	74.0	74.4	75.8
1254	69.6	70.6	71.4
1255	65.0	66.1	67.3
1256	53.5	54.9	56.5
1257	64.5	65.7	67.2
1258	58.5	59.2	60.0
1259	48.7	49.8	51.2
1260	77.6	78.3	79.4
1261	69.5	71.3	73.1
1262	32.8	33.0	33.0
1263	37.8	37.8	37.8
1264	55.5	56.5	57.8
1265	36.6	37.1	37.6
1266	44.0	44.1	44.1
1267	33.0	33.6	34.2
1268	33.1	33.4	0.5
1269	50.0	50.7	52.1
1270	56.0	56.5	57.2
1271	29.8	0.0	0.0
1272	29.5	29.9	30.0
1273	44.5	44.6	44.6
1274	55.1	56.3	57.7
1275	55.5	56.8	58.5
1276	66.0	67.0	68.1
1277	54.8	55.5	56.1
1278	23.6	0.0	0.0

c) Fertilised Plot T 1

TREE NO.	GIRTH76	GIRTH77	GIRTH78
2101	68.1	69.3	70.7
2102	28.2	28.2	28.2
2103	26.2	26.2	26.2
2104	21.2	21.4	21.4
2105	56.2	57.2	58.5
2106	61.1	61.7	63.1
2107	36.3	36.7	37.2
2108	34.3	34.4	34.5
2109	25.7	26.8	27.1
2110	50.6	51.7	53.0
2111	35.7	36.0	0.5
2112	72.8	74.0	75.6
2113	66.3	66.8	0.5
2114	65.8	66.7	67.1
2115	21.6	21.6	21.6
2116	60.2	61.2	62.6
2117	45.1	45.3	45.5
2118	38.9	39.5	40.2
2119	66.3	66.6	67.0
2120	94.0	96.1	98.0
2121	45.4	45.4	45.4
2122	75.5	76.9	79.2
2123	54.2	54.5	55.7
2124	70.7	72.3	74.0
2125	49.1	50.0	50.7
2126	67.8	69.1	70.8
2127	47.9	48.9	49.9
2128	24.2	24.2	24.2
2129	66.0	67.2	68.6
2130	56.5	57.4	59.0
2131	62.8	63.4	64.6
2132	35.3	36.5	38.0
2133	33.1	33.3	33.5
2134	72.0	73.4	74.1
2135	50.3	50.7	50.9
2136	49.2	50.7	52.3
2137	50.2	51.6	52.9
2138	34.9	35.6	35.6
2139	37.9	38.7	39.6
2140	40.6	41.0	41.8
2141	47.6	48.0	48.5
2142	70.4	71.9	73.9
2143	39.7	40.4	40.9
2144	63.6	64.5	65.2
2145	25.5	25.5	25.5

Table I c). continued,

TREE NO.	GIRTH76	GIRTH77	GIRTH78
2146	55.5	56.3	57.1
2147	26.0	26.6	26.8
2148	20.2	20.3	20.3
2149	40.9	41.1	41.4
2150	39.5	40.3	40.6
2151	61.2	62.4	64.5
2152	48.4	49.0	49.6
2153	39.4	0.0	0.0
2154	59.9	61.4	63.0
2155	45.8	46.3	47.0
2156	73.4	75.1	77.3
2157	43.4	43.9	44.3
2158	77.3	78.1	79.6
2159	30.2	30.2	30.2
2160	30.9	30.9	31.2
2161	42.6	43.2	43.9
2162	28.1	28.1	28.1
2163	41.4	41.4	42.4
2164	57.5	58.8	60.2
2165	68.2	69.5	70.2
2166	34.0	34.2	34.4
2167	47.3	48.6	49.5
2168	48.9	50.0	51.0
2169	69.4	69.8	70.4
2170	24.4	24.3	24.3
2171	74.0	75.5	76.9
2172	26.4	27.0	27.2
2173	56.9	58.3	59.0
2174	37.3	37.7	38.3
2175	22.5	22.5	22.5
2176	35.4	36.1	37.0
2177	21.6	21.7	21.7
2178	76.4	77.4	78.8
2179	48.6	49.7	50.4
2180	30.6	31.0	31.1
2181	72.5	74.3	75.4
2182	34.2	35.0	36.2
2183	52.3	54.1	56.4

d) Fertilised Plot T 2

TREE NO.	GIRTH76	GIRTH77	GIRTH78
2201	81.3	81.4	82.4
2202	54.8	55.9	57.0
2203	60.3	60.8	60.9
2204	27.6	28.2	28.6
2205	41.9	42.0	42.3
2206	29.8	30.1	30.1
2207	39.0	39.5	40.3
2208	28.7	28.8	29.6
2209	32.1	32.3	32.5
2210	75.2	76.0	78.1
2211	52.4	52.8	53.5
2212	35.4	36.2	36.9
2213	69.7	70.6	72.0
2214	23.8	23.8	23.8
2215	62.4	63.8	65.4
2216	48.8	50.2	51.8
2217	72.3	73.7	75.9
2218	26.1	26.3	26.6
2219	60.7	61.6	62.6
2220	78.7	79.2	80.2
2221	53.0	54.0	54.8
2222	72.1	73.0	74.3
2223	78.6	79.8	81.5
2224	85.1	86.3	87.8
2225	61.0	62.0	63.3
2226	52.8	53.5	54.4
2227	78.5	79.2	80.8
2228	71.5	72.9	75.0
2229	21.1	0.0	0.0
2230	42.6	43.3	43.9
2231	41.1	41.6	42.1
2232	53.0	54.1	55.3
2233	23.8	23.8	23.8
2234	51.3	52.0	52.9
2235	19.4	19.4	0.0
2236	33.6	34.0	34.3
2237	53.6	55.0	56.5
2238	29.5	29.7	0.0
2239	60.0	61.2	62.3
2240	30.4	31.1	31.6
2241	25.6	26.0	26.4
2242	52.4	53.8	55.4
2243	32.9	34.5	0.5
2244	55.7	57.1	58.8
2245	62.1	64.5	66.2

Table I d) continued,

TREE NO.	GIRTH76	GIRTH77	GIRTH78
2246	67.2	67.9	69.5
2247	83.1	84.6	86.9
2248	34.0	34.2	34.6
2249	69.4	70.0	71.6
2250	48.1	48.3	48.5
2251	35.5	35.6	35.6
2252	56.7	57.3	58.3
2253	56.5	57.9	59.6
2254	68.7	70.3	71.9
2255	64.9	66.1	0.5
2256	68.9	70.0	71.1
2257	52.5	53.3	54.4
2258	58.8	60.3	61.2
2259	17.0	17.1	17.1
2260	49.9	50.4	50.9
2261	51.3	52.4	53.7
2262	25.5	25.5	25.5
2263	58.1	58.6	59.5
2264	67.9	69.0	72.0
2265	37.5	37.7	38.3
2266	33.5	33.9	34.9
2267	25.1	25.1	25.1
2268	61.7	63.6	65.4
2269	50.3	52.1	53.4
2270	33.6	33.6	33.6
2271	69.1	70.5	72.1
2272	72.2	73.3	75.0

e) Sawdust-Sugar Treated Plot T 3

TREE NO.	GIRTH76	GIRTH77	GIRTH78
2301	41.6	42.0	42.6
2302	53.0	54.0	55.5
2303	62.5	63.2	64.3
2304	67.4	69.6	71.5
2305	68.7	70.1	72.2
2306	47.5	49.0	50.8
2307	15.5	15.5	15.5
2308	69.3	70.9	72.9
2309	54.2	55.5	55.8
2310	58.4	59.3	60.7
2311	36.3	36.6	37.2
2312	65.4	66.2	0.5
2313	21.9	21.9	21.9
2314	66.5	67.6	69.1
2315	79.9	81.8	83.8
2316	46.3	47.4	48.8
2317	62.8	63.5	64.4
2318	26.8	26.9	26.9
2319	87.8	88.6	90.3
2320	51.3	52.4	53.5
2321	67.8	68.9	70.6
2322	74.7	76.3	78.3
2323	41.7	42.4	43.1
2324	56.3	56.7	58.2
2325	63.0	63.9	65.7
2326	18.4	0.0	0.0
2327	72.7	73.8	75.2
2328	42.5	42.7	42.7
2329	59.4	60.4	61.6
2330	46.7	46.7	46.8
2331	33.5	33.5	33.5
2332	46.9	47.0	47.2
2333	45.6	47.2	48.6
2334	43.8	45.0	46.1
2335	59.2	59.8	60.9
2336	35.9	36.3	0.5
2337	45.0	0.0	0.0
2338	26.5	26.5	26.5
2339	23.2	0.0	0.0
2340	55.3	56.6	57.9
2341	72.5	73.7	75.6
2342	69.4	71.4	73.6
2343	59.8	60.3	60.8
2344	50.8	52.5	54.2
2345	63.3	64.0	65.4

Table I e). continued,

TREE NO.	GIRTH76	GIRTH77	GIRTH78
2346	82.5	84.0	85.9
2347	64.6	66.6	69.1
2348	68.1	68.8	70.3
2349	80.8	82.3	84.0
2350	60.6	61.5	62.4
2351	39.9	40.5	41.0
2352	50.8	51.2	52.5
2353	80.5	82.2	84.7
2354	57.2	57.5	57.7
2355	60.0	62.1	63.4
2356	45.2	46.0	46.8
2357	58.7	59.2	60.6
2358	46.6	47.0	47.8
2359	24.9	24.9	24.9
2360	52.0	53.0	53.7
2361	32.0	33.0	33.9
2362	64.5	66.8	69.0
2363	60.6	62.8	64.7
2364	60.6	61.8	63.1

f) Sawdust-Sugar Treated Plot T 4

TREE NO.	GIRTH76	GIRTH77	GIRTH78
2401	73.7	75.5	77.5
2402	50.1	50.5	50.7
2403	36.8	37.0	37.5
2404	26.8	26.8	26.9
2405	57.4	59.0	60.9
2406	42.3	42.3	42.3
2407	82.7	85.0	87.5
2408	50.2	50.3	50.8
2409	31.5	32.7	33.9
2410	39.3	39.9	40.5
2411	21.0	21.0	21.0
2412	31.4	32.0	32.3
2413	53.9	55.0	56.2
2414	49.9	51.0	52.2
2415	26.6	0.0	0.0
2416	50.4	50.8	51.1
2417	37.9	38.3	38.5
2418	72.3	73.9	75.5
2419	27.3	27.3	27.3
2420	36.2	36.6	36.9
2421	39.7	40.8	42.0
2422	44.0	44.2	46.4
2423	27.0	27.0	27.0
2424	50.0	51.1	52.5
2425	39.7	41.8	42.3
2426	57.2	58.0	60.0
2427	61.5	62.9	0.5
2428	44.5	44.5	44.5
2429	32.1	32.2	0.5
2430	29.3	29.8	30.0
2431	48.7	50.3	51.9
2432	59.8	61.3	62.8
2433	36.5	37.5	38.2
2434	24.8	25.3	25.4
2435	24.9	25.0	25.2
2436	17.1	17.1	17.1
2437	26.9	27.3	27.5
2438	61.3	63.2	65.2
2439	59.5	60.8	62.8
2440	17.4	17.4	0.0
2441	25.0	25.0	25.0
2442	63.3	63.4	63.6
2443	42.5	42.6	42.6
24432	25.1	25.1	0.0
2444	22.0	22.3	22.0
2445	81.3	82.8	84.9

Table I f) continued,

TREE NO	GIRTH76	GIRTH77	GIRTH78
2446	73.6	74.9	76.8
2447	37.2	37.3	37.3
2448	44.4	44.5	44.6
2449	51.2	52.9	54.5
2450	48.7	49.7	51.5
2451	19.2	19.3	0.0
2452	52.0	53.2	54.1
2453	66.0	67.3	68.9
2454	50.6	51.7	52.6
2455	47.2	47.6	49.2
2456	26.1	0.0	0.0
2457	55.3	57.0	59.3
2458	20.5	0.0	0.0
2459	59.7	60.8	61.8
2460	45.2	46.3	47.4
2461	21.8	0.0	0.0
2462	35.0	35.3	35.6
2463	25.0	25.3	0.0
2464	47.5	48.2	48.7
2465	64.4	65.5	67.0
2466	66.7	68.7	70.8
2467	57.7	59.9	61.7
2468	77.4	79.1	81.1
2469	57.8	59.4	60.5
2470	9.0	9.0	9.0
2471	52.5	53.5	54.3
2472	32.2	32.2	32.4
2473	18.2	18.2	18.2
2474	21.0	21.0	21.0
2475	44.9	45.8	47.2
2476	28.9	28.8	28.9
2477	35.9	36.6	37.3
2478	70.7	71.8	73.1
2479	49.3	51.0	52.8
2480	36.8	37.2	37.2
2481	33.4	33.5	33.5
2482	48.8	49.9	51.2
2483	42.0	42.5	42.7
2484	25.7	25.7	25.7
2485	80.0	81.7	84.0
2486	23.5	23.5	23.5
2487	20.4	0.0	0.0

Table II. Dry weights of different components in sample trees collected in 1977.

a) Major Components (kg., except for cones).

Tree No	Girth	Needle	Branch	Cone (g)	Crown	Bole	Dead Branch
1	20.0	0.66	1.12	.0	1.78	6.37	0.81
2	31.0	1.65	3.30	.9	4.96	17.26	1.64
3	37.5	2.46	3.96	19	6.43	28.27	3.81
4	40.5	2.81	4.12	0	6.92	33.64	2.95
5	42.6	4.45	6.62	36	11.11	36.90	8.63
6	48.7	8.69	10.45	0	19.13	53.23	5.78
7	50.5	7.72	13.94	43	21.70	58.52	1.04
8	60.7	12.14	15.65	0	27.79	82.66	7.13
9	69.0	12.72	29.38	0	42.18	94.92	6.69
10	80.7	17.46	54.79	4505	76.76	134.00	9.33

b) Needles and Branches of different ages (g).

Tree No.	Needle			Branch		
	First	Second	Third	First	Second	Third
1	337	259	64	49	51	1024
2	907	648	93	263	236	3299
3	1687	768	0	422	391	3960
4	1631	986	190	360	432	3323
5	2843	1522	87	448	433	5739
6	3574	2994	2118	828	795	8823
7	3911	3068	736	782	852	12303
8	5322	4056	2763	1407	1126	13113
9	6283	4058	2376	1661	1315	26407
10	8419	5432	3611	2639	2315	49837

c) Bole Bark and Wood Rings of different ages (g).

Tree No	Bark	Wood				
		Ring 1	Ring 2	Ring 3	Ring 4-10	Ring 11+
1	550	194	200	190	1482	3751
2	1594	1040	1215	1234	5928	6246
3	2911	2515	2790	2289	10438	7328
4	2930	1979	2016	2048	9264	15405
5	2912	2700	2900	2591	11449	14353
6	5410	5067	5490	4737	16282	17247
7	5088	4438	3841	3374	16305	25468
8	6289	5649	6795	5682	29581	28670
9	9023	6439	7275	7000	30978	34207
10	10907	10203	9156	8268	48300	47166

Table III. Dimension and dry weights of major components in sample trees collected in 1978 (kg., except for cones).

Tree No	Girth	Height	Needle	Branch	Cone	Bole	Dead Branch
1110	35.2	9.88	2.38	3.85	0	22.40	3.09
1103	63.3	13.46	9.65	19.18	458	91.51	9.26
1268	33.4	12.10	1.53	1.44	13	22.36	5.07
1207	64.0	14.02	8.86	17.72	510	85.72	10.21
2111	36.0	10.09	1.47	2.26	0	21.85	3.60
2113	66.8	14.00	8.56	18.18	1107	95.82	13.66
2243	34.5	11.28	1.77	3.18	0	22.64	0.59
2255	66.1	14.13	10.09	16.28	82	100.98	10.96
2336	36.3	9.55	1.05	1.62	0	19.87	3.77
2312	66.2	13.96	8.52	16.41	0	98.20	10.25
2429	32.2	9.84	1.76	5.96	0	18.49	3.38
2427	62.9	12.98	6.94	14.22	44	81.72	10.11

Table IV. Concentrations of N,P,K,Ca and Mg in various components (ppm). Values in brackets are standard errors.

a) 1977 samples

Components		N	P	K	Ca	Mg
Needles	1st.year	13106	1276	6091	1320	863
		(498)	(71)	(112)	(113)	(20)
	2nd.year	12873	1071	5908	2201	856
		(515)	(46)	(117)	(180)	(23)
	3rd.year	12788	986	5300	2823	798
		(524)	(49)	(105)	(281)	(24)
Branches	1st.year	10644	1283	4390	1381	864
		(224)	(21)	(60)	(24)	(14)
	2nd.year	9523	959	3842	1510	777
		(175)	(13)	(50)	(23)	(15)
	3rd.year	3518	611	1902	1466	666
		(117)	(7)	(22)	(30)	(13)
Bole Bark		3058	580	2104	2337	347
		(555)	(109)	(371)	(192)	(111)
Bole Wood	Ring 1	1394	245	2137	865	291
		(62)	(18)	(168)	(94)	(38)
	RING 2	1035	155	1374	782	218
		(36)	(10)	(72)	(111)	(49)
	Ring 3	862	129	989	807	180
		(30)	(6)	(34)	(123)	(40)
	Ring 4-10	680	98	854	825	186
		(28)	(7)	(39)	(145)	(35)
	Ring 11+	547	77	766	1056	258
		(25)	(5)	(34)	(242)	(36)
Cones		1322	128	866	546	122
		(108)	(4)	(32)	(47)	(3)
Dead Branches		2416	262	310	740	70
		(353)	(9)	(32)	(211)	(17)

b) 1978 Control samples.

Components		N	P	K	Ca	Mg
Needles	1st.year	11453	1352	7763	1343	759
		(461)	(30)	(203)	(306)	(49)
	2nd.year	12372	1173	6506	2534	770
		(731)	(22)	(144)	(709)	(40)
	3rd.year	11429	1122	6419	3955	799
		(607)	(29)	(198)	(1303)	(78)
Branches	1st.year	11187	1386	4866	1693	736
		(129)	(53)	(248)	(168)	(54)
	2nd.year	9720	1016	4609	1959	675
		(256)	(34)	(287)	(202)	(55)
	3rd.year	2986	274	1933	1828	418
		(141)	(19)	(130)	(106)	(31)
Bole Bark		3071	531	3185	2270	343
		(619)	(140)	(1055)	(288)	(147)
Bole Wood	Ring 1	1115	157	1639	648	102
		(66)	(16)	(159)	(87)	(10)
	Ring 2	856	101	903	586	74
		(64)	(8)	(59)	(62)	(11)
	Ring 3	822	105	950	619	73
		(54)	(7)	(70)	(68)	(8)
	Ring 4-10	653	82	842	873	82
		(22)	(4)	(40)	(24)	(7)
	Ring 11+	652	83	866	1003	156
		(55)	(17)	(136)	(68)	(21)
Cones		1663	249	820	301	145
		(44)	(41)	(21)	(45)	(4)
Dead Branches		2613	263	264	551	42
		(294)	(13)	(2)	(200)	(3)

c) 1978 Fertilised Plot samples

Components		N	P	K	Ca	Mg
Needles	1st.year	12515	1281	6536	1520	746
		(381)	(40)	(436)	(310)	(57)
	2nd.year	13034	1174	5327	2723	771
		(630)	(54)	(384)	(444)	(59)
	3rd.year	12388	1118	5268	3402	755
		(181)	(41)	(128)	(611)	(84)
Branches	1st.year	11861	1351	4516	1308	740
		(586)	(69)	(227)	(232)	(31)
	2nd.year	9897	973	3624	1626	628
		(619)	(32)	(250)	(178)	(39)
	3rd.year	3433	259	1590	1425	465
		(451)	(36)	(140)	(167)	(27)
Bole Bark		2944	464	1610	2086	234
		(782)	(131)	(356)	(556)	(130)
Bole Wood	Ring 1	1510	195	1916	468	112
		(122)	(34)	(264)	(37)	(29)
	Ring 2	970	118	1112	620	83
		(118)	(14)	(82)	(93)	(13)
	Ring 3	891	110	971	640	89
		(101)	(12)	(77)	(102)	(14)
	Ring 4-10	759	103	991	678	102
		(47)	(20)	(185)	(106)	(16)
	Ring 11+	675	79	735	887	163
		(30)	(7)	(38)	(61)	(13)
Cones		1656	236	764	294	139
		(37)	(29)	(24)	(42)	(5)
Dead Branches		2525	256	257	593	48
		(61)	(4)	(7)	(13)	(7)

d) 1978 Sawdust - Sugar Treated Plot samples

Components		N	P	K	Ca	Mg
Needles	1st.year	10377	1330	7390	1429	840
		(301)	(46)	(626)	(384)	(53)
	2nd.year	10359	1174	6216	2803	896
		(422)	(37)	(381)	(1064)	(56)
	3rd.year	10008	1101	5301	3878	885
		(791)	(50)	(364)	(1399)	(15)
Branches	1st.year	9473	1147	4199	1260	615
		(247)	(30)	(165)	(173)	(33)
	2nd.year	9050	879	3824	1491	665
		(292)	(10)	(105)	(139)	(48)
	3rd.year	4148	321	1872	1457	522
		(355)	(14)	(112)	(124)	(36)
Bole Bark		2729	463	2344	2489	280
		(610)	(112)	(515)	(197)	(91)
Bole Wood	Ring 1	1086	170	1851	681	95
		(92)	(36)	(267)	(70)	(4)
	Ring 2	881	112	975	753	73
		(70)	(13)	(133)	(66)	(4)
	Ring 3	794	103	964	646	77
		(81)	(10)	(148)	(118)	(5)
	Ring 4-10	676	85	832	855	98
		(58)	(8)	(36)	(130)	(13)
	Ring 11+	589	56	641	1067	118
		(27)	(4)	(71)	(128)	(9)
Cones		1678	257	863	280	147
		(32)	(12)	(31)	(41)	(5)
Dead Branches		2692	270	261	432	42
		(179)	(4)	(5)	(33)	(3)

Table V. Sampling occasion, date, rainfall and throughfall.

Sampling occasion	Date	Rainfall (cm)	Throughfall (cm)
0	23/6/77		
1	21/7	3.37	2.03
2	18/8	4.47	2.89
3	15/9	8.75	5.15
4	13/10	11.31	7.44
5	10/11	13.78	8.32
6	8/12	2.94	1.11
7	5/1/78	6.95	4.76
8	2/2	9.11	6.10
9	2/3	6.48	4.20
10	30/3	10.39	5.71
11	27/4	2.89	1.19
12	25/5	4.29	2.80
13	22/6	2.93	1.87
14	20/7	4.25	2.39
15	17/8	12.74	8.62
16	14/9	10.01	7.28
17	12/10	5.08	2.70
18	9/11	3.25	1.77
19	7/12	11.79	7.53
20	4/1/79	12.47	8.02
21	1/2	1.97	1.24
22	1/3	0.93	0.46
23	29/3	8.89	5.50

Table VI. Sampling occasion, date and 4-weekly production of needle and total litter ($g/0.05m^2$).

Sampling occasion	Date	Control Plots		Fertilised Plots		Sawdust-treated Plots	
		Needle	Total	Needle	Total	Needle	Total
0	26/5/77						
1	23/6/77	0.754	1.107	0.818	1.193	0.774	1.113
2	21/7	1.464	1.924	1.097	1.677	1.309	1.927
3	18/8	0.501	0.708	0.364	0.617	0.386	0.791
4	15/9	5.006	5.111	4.241	4.404	4.310	4.620
5	13/10	8.529	9.270	7.750	8.306	8.433	8.982
6	10/11	0.877	1.472	0.781	1.084	1.032	1.421
7	8/12	0.612	0.906	0.583	1.068	0.828	1.217
8	5/1/78	0.224	0.385	0.219	0.724	0.227	0.725
9	2/2	0.423	0.891	0.381	1.256	0.641	1.376
10	2/3	0.050	0.227	0.047	0.264	0.067	0.532
11	30/3	0.187	0.369	0.191	0.406	0.143	1.006
12	27/4	0.051	0.134	0.034	0.415	0.033	0.367
13	25/5	0.107	0.315	0.105	0.489	0.075	0.316
14	22/6	1.584	2.785	1.389	3.759	1.512	2.182
15	17/7	0.283	0.667	0.206	0.624	0.224	0.495

Table VI. continued,

Sampling occasion	Date	Control Plots		Fertilised Plots		Sawdust-treated Plots	
		Needle	Total	Needle	Total	Needle	Total
16	17/8	0.602	1.492	0.719	1.034	0.501	1.716
17	14/9/78	4.944	5.226	5.686	5.999	4.417	5.270
18	12/10	6.306	6.862	6.721	7.248	6.916	7.362
19	9/11	1.373	1.655	1.331	1.576	1.595	1.946
20	7/12	1.004	1.388	1.130	1.805	1.408	2.079
21	4/1/79	0.158	0.536	0.223	0.753	0.256	0.566
22	1/2	0.148	0.333	0.340	0.682	0.257	0.475
23	1/3	0.103	0.165	0.151	0.175	0.075	0.078
24	29/3	0.502	1.318	0.539	1.044	0.490	0.694

Some technical problems encountered in the study

This addenda on some technical problems and suggestions to overcome them is included for the benefit of those wishing to repeat such a study.

The sample plot size was restricted to 0.05 ha by the limited area of the study site. Although this was found to be adequate, larger plots, up to 0.1 ha may be preferable, depending on the variability of the crop.

Some glass bottles used to collect rain-water broke when the water in them froze over. To overcome this and to reduce the growth of algae, the use of plastic bottles within black plastic bags is recommended.

The wide range of concentrations found in all the different tissues posed the main problem in the chemical analysis of the samples. To reduce the range, larger wood samples (0.2g) were used, compared to needle samples (0.1g). The size of the samples could not be increased further as the digest tubes and digestion block were designed to handle only small samples ($<$0.5g). To cover the entire range of concentrations found, two sets of standards which overlap slightly were used. For even lower concentrations,as was found in the rain-water, the main dilution stage in the analyses of N and P were dispensed with and dilute alkali (NaOH) added to correct the pH. While the determination of K was relatively simple, the determination of Ca and Mg required the addition of Lanthanum to reduce interference from other ions; but it was generally found that freshly diluted samples gave the most consistent results.